

LEARNING AND ORIENTATION IN ANTS

STUDIED BY MEANS OF THE MAZE METHOD

BY

T. C. SCHNEIRLA

DEPARTMENT OF PSYCHOLOGY, NEW YORK UNIVERSITY (WASHINGTON
SQUARE COLLEGE)

A DISSERTATION

SUBMITTED MAY, 1928, IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF SCIENCE IN PSYCHOLOGY
IN THE UNIVERSITY OF MICHIGAN

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I. INTRODUCTION

A. Foreword and statement of problem

The question of ant orientation, especially in its relation to food-getting, has never lacked scientific attention. Since Bonnet (1745) and Latreille (1802) made their classic observations and crude tests, investigators have been interested mainly in the control of orientation by the receptors. Yet there has been all too general a tendency to place emphasis upon the importance of the one or the other end-organ, and to minimize or neglect not only the possibility of functional integration among the receptors, but also the likelihood that their rôles may vary in importance from one time to another in the same situation.

Previous to 1910, investigators appear to have taken for granted the fact that ants 'profit by experience' in their orientation, without going much deeper into the matter than to recount instances of next-behavior and food-getting behavior that seemed

to indicate 'plasticity.' The work of Fiedle and of Turner, early in the present century, clearly showed the need for thorough study of ant learning. Shepard (1910-1914) developed a maze technique for examination of the problem, and used the method to good advantage in a series of general studies. The methods of the present experiments are largely based upon his procedure.¹

Investigation of learning in any animal form must first concern itself, generally and comparatively, with the effective stimuli. Within the past fifteen years the study of the receptors involved in the orientation of various species of ants has reached its highest development in the experimentation of R. Brun. The maze situation enables close examination of this problem, under rigid control.

Once the above question is fairly well solved, we need to find the important characteristics of the animal's ability to learn, and the conditions under which the learning varies in efficiency. The present investigation represents a general examination of the course of learning in two species of *Formica* (note 14), not considering the learning apart from the functioning of the different receptors.

The present paper involves a discussion of the mechanics of orientation in the maze, in which the writer endeavors to show the importance of the kinaesthetic and contact receptors. In close relation to this phase, a considerable portion of the study is devoted to the importance of maze pattern for the course and rapidity of learning. Further, we report experiments dealing with the mastering of a maze the pattern of which is locally changed following original learning, and others concerned with the ability of ants to adapt to altered visual conditions. Emphasis is placed upon the way in which deviating responses ('errors') are eliminated in the course of maze habituation.

Since an examination of the problem cannot be restricted to any one phase, at the present time, the investigation had best be termed 'an experimental study of ant learning.'

¹ The writer wishes to express gratitude to Prof. J. F. Shepard for the constant stimulus of his scientific example, and for the value of his previous work with ants, which provided the first suggestion and main basis for the present experiments.

B. The general literature

As noted above, the first problem to be solved in studying the orientation of any animal concerns the rôle of the receptors in the activity. It is interesting to note how students of ant behavior first emphasized the most obvious sensory control, then came to give some attention to other receptors, and finally have come to a measure of recognition of the plasticity that characterizes the function of the receptors in the control of orientation.

Bonnet (1745) reported the first experimental investigation of ant orientation. His 'finger experiment,' which representatively consisted in rubbing the finger across the path followed by ants of a smaller species (*Lasius*), resulted in the ants stopping on either side of the altered area. This indicated a break in what was assumed to be a trail consisting of some chemical substance laid down by the ants in passing along the path, rigidly followed by them. For some time thereafter this conclusion was applied to all species of ants, and it has persisted as the popular explanation.

Somewhat later it was found that the 'chemical trail' explanation would not suffice to explain the orientation of all species of ants. In the course of his observations on *Polyergus rufescens*, P. Huber (1810) incidentally found that scraping away the surface earth for some distance about the nest entrance produced no great disturbance, and did not prevent passage across the area. Forel (1864) reported a similar failure of the finger-experiment for *Formica rufa*. Fabre (1879) found it possible to make many changes (rubbing with 'odorous substances,' sweeping off the surface, covering with paper, etc.) on the surface of the trail followed by *Polyergus rufescens* on its raids, without greatly disturbing it. Both Forel and Fabre denied any rigid following of a chemical trail in this species. Forel indicated that vision might play a considerable part, and Fabre later suggested the operation of a well-developed "place memory."

Lubbock's experiments (1876-1888) enabled placing greater emphasis upon the importance of vision in orientation.

After *Lasius niger* ants had been carrying larvae to their nest for some time, across a paper bridge which led over his circular experimental table (rotatable in three concentric sections), Lubbock found that rotating the middle section of the bridge through 180° caused the ants upon it to turn against the rotation and proceed in the original direction.² When the ants were covered with a box during the turning, only about one-third of them resumed the first direction, and these did so hesitatingly. Working this through, Lubbock found that if the candles used for illumination (two of them on one side of the table) were rotated with the table, the ants did not make the compensatory turn, but that if the candles were moved to the opposite side, without the table being turned, most of the ants reversed their direction of progress on the path. This shows that the position of the light was the important factor. Lubbock concluded that the ants were "greatly influenced by the direction of the light."

However, Lubbock was led to state that *Lasius flavus* "guides itself but little by sight," since changes in the position of an upright pencil, used in some experiments as marker of the nest and in others as marker of the larva-cup, did not seem to influence the ants. The well-known experiment, in which *L. niger* ants were allowed to pass to and from the larva-place over a paper trail leading between five pairs of wooden bricks and under a paper tunnel, resulted in the ants following the paper trail in the same manner regardless of changes made in the position of the bricks or tunnel. This was taken to indicate the absence of vision for nearby objects.

Hence Lubbock clearly recognized that factors other than an 'odor trail' play a part in orientation. However, in 1898 the first of Bethe's papers forcibly called attention to the subject of the chemical trail, and in the general concentration upon his theory ('ants are reflex machines automatically following a polarized odor trail') the important conclusions of Lubbock, Fabre and Forel were neglected for some time.

Bethe worked with *Lasius emarginatus* and *L. niger*, species that characteristically orient to a considerable extent according to the chemi-

² Lubbock originated the 'rotation technique' later utilized by Bethe, Brun and others.

cal features of their paths. A typical experiment involved a trail over a narrow rotatable zinc strip 16 cm. in length, leading from the nest to an aphid stock. After the ants had passed over this trail for some time, Bethe performed Lubbock's experiment (turning the mid-section of the path through 180° while ants were crossing it). This resulted in an evident stoppage on both ends of the rotated section, not only of ants coming to the section from nest or aphid colony, but also of those remaining on the path during the rotation.

In addition, it was found that three adjoining sections of pathway could be interchanged in any order without the slightest disturbance, but that if one of them had been rotated during the interchange a noticeable disturbance would result.

To explain his results Bethe formulated his "Polarisationstheorie" and postulated the "Heimkehrreflex." According to the theory, an 'outward' or a 'nestward' trail is chemically polarized, and is followed in a rigid, reflex manner by the ant. Hence it is impossible for an ant to pass 'outward' over her 'nestward' trail, or the reverse. According to the "Heimkehrreflex" postulation, unladen ants automatically set out upon their trails from the nest, while laden ants reflexly assume the trail to the nest, the carrying of a load being sufficient to set off the behavior (see Appendix II).

Bethe has been vigorously and generally criticized for the somewhat far-fetched nature and application of his theories and assumptions, and for his inadequate knowledge of ant behavior. Nevertheless, the writer believes there is greater value in his treatment of the subject than most critics have been willing to grant.

Wasmann (1898, 1909) considered Bethe's interpretation too simple and misrepresentative. Recognizing the validity of most of Bethe's results, Wasmann thought their explanation to be a qualitative polarization of the paths,—i.e., the outward path must possess a characteristic "Nestgeruch," the path to the nest a "Futtergeruch,"—not a radical departure from the basic implication of Bethe's theory. Wasmann added the assumption that the ants must be capable of distinguishing through delicate antennal organs the 'odor form' of their own footprints. He assumed this 'odor form' different for paths in the two directions,

since the traces left by the tarsal segments of the legs must be spatially different.³

That many species do not orient by closely following an odor trail was again shown by Wasmann's failure to find any great disturbance when the modified finger-experiment was performed for *F. praetensis* and *F. rufa*. In other experiments (1901) ants were made to pass from their nest to a secondary nest through a bent glass tube. The tube was rotated through 90°, causing the ants to hesitate and stop at the bend, a phenomenon Wasmann thought due to the altered relationship of the direction of turn and the direction of illumination, rather than to a break in a chemical trail.

Forel (1900) maintained that ants, in palpating objects along the path with their antennae, obtain 'topochemical' impressions which are effective in guiding further passage over the same route. These impressions, in a continuous series, were believed to form a complex mnemonic organization. After covering with opaque varnish the compound eyes of some *F. praetensis* individuals and extirpating the antennae of others, Forel reported that in the first case the ants followed the trail with great difficulty, but were able to find the nest, whereas in the second the ants were totally unable to find their way. The 'varnish experiment' suggests the importance of vision in the homing of this species; and in the second case the results may have been due (in part) to loss of the antennal olfactory organs, as Forel concluded.

In 1904 Piéron stressed another orienting factor. His well-known experiment involved the transfer of a homegoing, laden *Aphaenogaster nigra* individual, on a prepared portion of her pathway, to a point a "certain distance" at the side of the established route. Such an individual usually responded by continuing in the former direction, running parallel to her original trail, until she had passed through a distance approximately equal to that she would have travelled to reach the nest on the

³ Brun has shown the untenability of this view. For progress in one direction the tarsal segments of the front and rear legs point in opposite directions; and furthermore, the single trail of but one ant is a greatly complicated mass of traces, scarcely permitting the discrimination demanded by Wasmann's theory.

former path. After stopping, the ant wandered about. This phenomenon was believed attributable to the operation of a "memoire musculaire," which was assumed to function as a *general guide* in the orientation of ants, even to enable reversal on the homegoing journey of the series of 'muscular impressions' gained on the outgoing passage.

Concerning the specific orienting factors, Piéron found wide inter-species differences. In the case of *Aphaenogaster*, certain experiments showed the tactile sense of most importance in furnishing "points de repère," while for *Formica cinera* vision was of most consequence. *Lasius fuliginosus* was found mainly dependent upon olfaction for specific 'reference points.'

The importance of the individual wanderer was emphasized by Cornetz (1910), in his detailed investigation which involved the study of trails made by ants of many species. The following is a description adapted from Cornetz's observations of "solitary forager" ants.

A *Myrmecocystus* leaves the nest opening to move a short distance in a single general direction, halts on a "tournoiement de recherche de provende" (search for food), and then continues in the original general direction, with occasional "recherches de provende," until food is obtained or failure long continued. She then assumes a direction roughly the reverse of that taken on the outgoing trip, and follows this without any marked deviations, until the nest vicinity is reached. Finally, on arriving near the nest, certain exploratory "tournoiments de Turner" (irregular, circuitous movements first reported by Turner) are made. In the latter series of wanderings, a visual (olfactory, contact) memory for disconnected features of the immediate nest vicinity may be effective in aiding entrance to the opening. . . . In other cases the ant passes out from the nest by maintaining two or more general directions in succession, interspersed with "tournoiments de recherche," and on the return reverses (roughly) these general directions. The latter type of course is not seen as frequently as the former.

Cornetz emphasized the importance of the individual wanderer as the primary orientation phenomenon, whose path provides the basis for the establishment of a collective trail. For example, in *Myrmecocystus bicolor*, the olfactory characteristics of

the individual worker's trail probably aid the other ants to follow it.

An 'inner direction sense' was postulated by Cornetz to account for the ability of the solitary worker to maintain one or more general directions when on a foraging expedition.⁴ The following cases typify the evidence he has presented.

. . . . A *Myrmecocystus* was carried from the nest to a "strange locality" about 75 M. distant. This place, an open shed facing away from the sun, (presumably) did not permit orientation on the basis of the direction of the sun's rays. In fact, due to reflection, the direction of greatest illumination was opposite to that of the sun's rays. Nevertheless, when the ant was released, after a short period of wandering she passed to the nest.

. . . . A homegoing ant was transported to the opposite side of the nest, into a 'strange' locality. She continued to run in the direction assumed before she was transported, although this took her directly away from the nest.

. . . . Transport experiments conducted in "deep forest twilight," or at dusk, nevertheless gave results similar to the above.

. . . . In the twilight, *Tapinoma erraticum* individuals foraging on a bone were covered. Ants were seen to enter under the edge of the cover from two different directions. The bone and the cover (a pan) were then transported 5 M., and the bone was rotated through 90°. Ants coming out from under the cover were not disoriented, but set off in one of the two directions, as before.

Results such as the above were taken as evidence for the existence of "an internal factor that could not have been either visual, olfactory, or tactual in nature." However, in all of the tests a satisfactory visual control seems to have been lacking. In fact, Santschi and Brun regard the results as offering better evidence for the influence of known factors, and for vision in particular, than for Cornetz's theory.

Cornetz has emphasized his finding that an ant picked up at the nest and transported to a distant place cannot return to the nest as well as can an individual that has first made the trip from

⁴ Santschi asserted that excellent proof for the influence of vision was offered by many of Cornetz's experiments.

the nest to that place.⁵ This is taken as evidence for the influence of an internal impression (not muscular, as described by Piéron) obtained on the outgoing journey, an impression which serves to guide the ant until the scattered sensory cues—visual and olfactory, the latter less fragmentary in nature—furnished by the immediate nest vicinity become of assistance.

Santschi (1911), by means of his *mirror experiment* (an adaptation of the Lubbock 'candle shifting' experiment), demonstrated the importance of the direction of illumination for orientation in the open.

A portion of *Tapinoma* (*Messor*, *Myrmecocystus*) trail was shielded from the rays of the sun, which were then reflected onto the shaded area from the opposite side by means of a large mirror. Unladen ants coming along the path were observed to hesitate at the border of the differently illuminated zone, while the laden ants promptly turned around and retraced the trail until the normally illuminated area was reached. The ants all resumed their former direction of progress fairly soon after the shield and mirror were removed. . . . The effect of the experiment decreased when it was performed on portions of pathway closer to the nest, but was most pronounced when there was no constant wind, when the sun was nearer the horizon, and when there were no outstanding large objects in the vicinity.

Experiments later performed by Santschi indicated the possibility of orientation according to the position of larger objects in the vicinity.

When the mirror experiment was successively performed for ants of various species, a *Camponotus* worker was observed to correct her passage by means of a nearby date tree, but lost this cue and was disoriented when she descended into a depression; an *Aphaenogaster* individual oriented according to the position of a wall; and a *Messor* forager recovered her original direction with the (apparent) help of a large pile of sheaves. In contrast, when the experiment was carried out for a

⁵ This involves some confusion with regard to the possible influence of learning in the two cases. The superior homegoing ability of the ant that has made her own outgoing trip (as compared with the ant transported to the place from the nest) may not be due to the effects of the one trip out from the nest, but to an undetermined number of trips.

stream of *Messor barbarus* individuals following a narrow trail, the reflected light produced an eddy in the procession, but none of the ants turned around.

Further, a forager was disoriented by being covered with a vessel perforated in such a way as to allow only diffuse light to enter it, but was not disturbed in her passage toward the nest by being covered with a jar of clear glass. These results were taken as further proof for the importance of directed illumination as a guide in orientation.

Santschi suggested that vision can be a guide in one of several ways, depending upon whether the effective stimuli are furnished by large well-illuminated nearby objects, by the relationships of lighted and shadowed zones, or by the direction of the sun, whether or not its rays are diffused through clouds or through the branches of trees. Night foragers may depend upon the illumination furnished by the moon, or upon the principal stars. Vision is not ruled out by the fact that an ant can maintain a principal direction on her outgoing journey, and reverse this in passing back to the nest, since 'if an ant on the out-journey had the sun in the rear facets of the left eye, on the return she would place her body so that the sun's rays would stimulate the forward facets of the right eye.'

Perhaps the most important series of studies on the orientation of ants is that made by R. Brun (1914-). A somewhat detailed presentation of his work will give a systematic review of the results that have been obtained by the European experimenters.

Brun's experiments were conducted both in the field and in the laboratory. For the first type his garden was used, a large sandy space surrounded by a lawn, gravel walk, trees, and other features. In the laboratory he employed an improved 'Lubbock table,' the top of which (circular, in three concentric pieces) could be tilted at any angle or turned about its center. From an artificial nest the ants crossed this table on a narrow paper bridge which led to larvae or honey. The visual situation (direction of light) was controlled by the "Methode der bipolaren Beleuchtung," which involved the placing of two candles on opposite sides of the experimental table.

In the following experiments dealing with the 'chemical trail,' the deposited traces were found not rapidly evanescent, even for lightly travelled paths. This held for conditions involving changes that must have radically altered the chemical features of the pathways.

Lasius niger individuals were allowed to wander to honey through a system of tubes. By pushing in or pulling out the smaller tubes, it was possible either to cover a section of previously laid-down pathway or to expose a section of fresh tubing. Pushing one tube into another to cover a section of established pathway had no great effect, but the ants were temporarily disturbed when a new area of tubing was exposed. The reintroduction (after an interval) of a portion of well-established pathway brought only a slight and momentary disturbance. After a tube had been thoroughly washed, the odor trail seemed almost completely obliterated. . . . Brun turned over part of a heavily travelled paper pathway, but the ants crossed as before, without disturbance, suggesting that the deposited chemical substances had settled into the paper.

Studies of *Lasius fuliginosus* on 'odor paths' brought the following results, which we present with Brun's interpretation.

1) Orientation is by no means exclusively controlled by odor, but also depends upon "related factors"—direction of light rays, general topographical relationships, length of the pathway, etc.—which the ant "engraphs in globo" (associates as a whole).⁶ When set down upon a known or unknown path the ants do not set off at once, but will make a few wandering ventures before the influence of the related factors permits orientation.

. . . . Ants (*L. fuliginosus*) passing to honey across a bridge of white paper, formed a "well-established honey trail." Individuals taken from the nest and set down upon the middle of this path hesitated

⁶ Semon was the originator of the mnemonic terminology employed by Brun. The following two laws represent the basis of the Semon theory:

The law of engraphy—"All simultaneous excitement in an organism forms a connected stimulation-excitement complex, which as such works engraphically, i.e., leaves behind a connected engram-complex which in so far forms a whole."

The law of ephory—"The partial return of the energetic situation which formerly worked engraphically operates ephorically on a simultaneous engram complex."

for a time before starting off. The ants starting for the platform end seemed to hesitate under way, while those passing toward the nest did not.

. . . . A larva-trail was established; then ants were taken from the nest and set down in the middle portion of the pathway near a heap of larvae ("Larvenabholen aus der Mitte" experiment). Individuals so set down went off impartially in either direction, usually in the direction faced when deposited. However, when one side of the paper path was turned up to form a 5 mm. high railing, not many ants would take the 'false' direction (toward the platform), and even these would soon turn back toward the nest. Disorientation returned when the railing was removed, and the ants reversed their direction when the railed portion of the bridge was turned through 180°.

2) A 'food trail' (honey) is polarized in the sense of being olfactorily different at various points, but an established 'larva trail' is completely apolar. (Lubbock worked with the latter, and hence did not observe the 'polarization phenomenon' of Bethe.) In experimenting on this point, when portions of honey-trail, or of larva-trail, were subjected to rotation or to interchanging of parts, the following results appeared.

. . . . On honey-trails the Bethe-phenomenon (p. 5f.) was evident, and appeared more definitely when the pathway changes were made for the nest end of the homeward trip than when they were made for the platform end. Interchanging pieces without rotation on such trails gave disturbing effects at both ends of the path, and with rotation of sections the reaction increased in proportion to the length of the rotated stretch of pathway.

. . . . On larva-trails, the disturbance occasioned by the performance of the above experiments was negligible.

. . . . If widely separated portions of a honey-trail were exchanged, the Bethe-phenomenon was more evident than when the pieces were close together on the pathway.

Claparède (1903) had pointed out that since the aphid trails of Bethe's *L. niger* (p. 5) led across a flat zinc surface, there was no possibility for the influence of Forel's topochemical sense, granting its existence. However, in 1916 Brun reported the following experiments as evidence for the Forel theory.

Over the experimental table, under bipolar illumination, a paper bridge led to a larva-place. A larva-trail was established, the ants

(*L. fuliginosus*) being allowed to carry larvae to the nest for twenty-four hours, and then the "Larvenabholen aus der Mitte" (see above) experiment was successively conducted for the following situations:

a) A bridge whose surface on the half nearer the platform had been stamped with round upward projections;

b) a bridge the nest end of which had been stamped with pinholes arranged in lengthwise rows, the platform end with pinholes arranged in squares;

c) a bridge whose surface was covered with an oily violet perfume marked in crosswise ovals for the nest end, and in circles for the platform end; and

d) a bridge covered with pine needles fastened lengthwise on the nest end, and crosswise on the platform end.

It will be remembered that the "Larvenabholen" experiment, when conducted under conditions involving a smooth paper bridge, had resulted in an equal choice of the two directions by ants coming from the nest to the larva heap. Under the new conditions, Brun reported that a majority of the ants passed 'correctly' back to the nest in every case, while of those starting 'falsely' for the platform end many turned back under way. However, ants without antennae passed in equal numbers toward the opposite ends of the path.

It was Brun's conclusion that condition a) had been mastered through "purely stereotactile" discrimination; condition c) through "thigmo-olfactory" discrimination and condition d) by means of a "topochemical" discrimination—Forel's contact-odor sense.⁷

Many species (*Formica*) do not characteristically travel on paths, but over 'thoroughfares' (see note 22). Under these conditions, Brun found (1914) that orientation is almost completely independent of deposited chemical substances. "Kin-

⁷ The writer finds it difficult to understand why the discrimination in condition 'c' could not depend upon a quantitative difference between the chemical stimuli presented by the two alternatives, rather than upon the spatial arrangement of the circles and ovals; and why condition 'd' could not be mastered by means of the tactile differences alone. It is clear that tactile discrimination was involved in some of these cases, and olfactory discrimination in others, but it cannot be agreed that the experiments were controlled in such a way as to prove that the two factors functioned *together* (in any instance) in the closely integrated manner required by the Forel theory. (The extirpation of antennae is not a good control of olfaction.)

aesthetic engraving" appears to play an essential part, but not according to Piéron's description of its function. On the whole, the results of the following experiments led Brun to place the greatest emphasis upon vision.

A *Formica praetensis* individual, when transported to a place some distance from her trail, continued in the original direction when released, although she now passed directly away from the nest (as Cornetz found). Sometimes, however, the ant "appeared to notice that she was going incorrectly, and turned around."

When the experimenter stood in front of the nest entrance the ants were disoriented. The disturbance was at first wrongly attributed to the covering of a nearby bush.

Repetition of Wasmann's experiment—taking the ant from the thoroughfare, rotating her in a box (Brun's addition), and releasing her at the same place—resulted in *Formica rufa*, *sanguinea*, *fusca*, *cinerea* and *rufibarbis* setting off at once in the earlier direction.

Forel's experiment—forward and backward transport to different parts of a winding course—and Piéron's experiment often disoriented the ants, especially "on heterogeneous terrain." However, the 90° or 180° turning of a piece of carpet which had been incorporated in a path did not seriously disorient ants that were on it when it was rotated.

According to Brun's interpretation of these and similar results for orientation on thoroughfares, the ants depend chiefly upon the "globalized local topochemical and visual complexes, in union with a sensorily reversible light-engram" (direction of illumination), although at times they may form "Wegbilder." Hence there is every possibility that the presence of large objects ("guiding visual landmarks") and other terrain peculiarities may be engraved, and used by the ants in their orientation. In addition

"The fact that higher *Formica*-varieties are able, on transport to a vicinity not hunted over for weeks or months, to reorient themselves quickly and with certainty on the shortest way toward the nest, indicates the existence of a general spatial memory (Ortsgedächtniss) attributable to the differentiated single engrams" (visual and topochemical).

The importance of the "sensorily reversible light-engram" was demonstrated by the "Fixierversuch" (confinement experiment), as follows.

A *Lasius niger* ant under way toward the nest was shut under a box for a period of two (to four) hours. When released, after a brief hesitation, the ant set off in her former virtual (direct) orientation, though this now took her on a line diverging from the direct course to the nest by an angle equivalent to that through which the sun had moved during the period of confinement. This fact held for periods during which the sun had moved through angles as great as $23\frac{1}{2}^{\circ}$, and for courses at right angles to the solar illumination, or away from it, etc. The phenomenon was evidenced with considerable rigidity by ("niederen") species such as *L. niger*, but was not very evident when the experiment was performed for *F. sanguinea* and other ("höheren") species.

The conclusion drawn by Brun was that in the case of the latter species the ability to orient according to large nearby objects and terrain peculiarities usually makes it possible to dispense almost entirely with the more rigid type of visual guide. This, of course, depends upon conditions.

A further test (1914) of the influence of vision, the "Lubbock candle experiment in closed apparatus," gave results which indicate the functional relationship that exists between the visual and the kinaesthetic factors.

F. rufa individuals were allowed to get food from a nest connected with their own by a glass tube. When a previously stationary candle was changed 90° in position, the ants wandered nearest that side of the secondary nest which was 'correct' according to the original position of the light. (A *rufa* "even put her antennae into the mouth of the tube without knowing this as the exit!") When Brun returned the candle to its original position, the ants readily found the exit to the home nest. Changing the candle 180° from the original side caused the ants to repeatedly enter a tube on the opposite side from the home nest. Turning the entire apparatus through 45° , 90° , and 180° produced virtual orientation in each case, although the new conditions of illumination led to behavior quite at odds with the actual position of the exit tube.

If the apparatus remained covered, the rotation did not produce such effects. Upon coming from the secondary nest into the light, the ants

were seen to hit upon a direction of progress which was the resultant of the "false" direction of the tube (under rotated conditions) and the true road to the nest, and to maintain this "compromise direction" even through a considerable distance, then to correct it in the process of a curving course. (This "compromise," Brun believed, was actually the resultant of two sensory controls,—a visual, (or localized "light-engram") and a topo-kinaesthetic. As long as the above difference was not too great,—less than 45° , probably—the two could make successful concurrence, but if greater, the "visual engram" would dominate.)

Szymanski (1911) had taken the results of his deviation experiment ("Ablenkungsversuch") to indicate the existence of a kinaesthetic perception of angles ("kinetischen Winkelvorstellung"), similar to the concept later developed by Santschi. Brun (1914) repeated the experiment, but offered a different interpretation of the results.

After Szymanski, the constrained course experiment ("Zwangslauf") consisted in forcing the ant from her homegoing trail with the finger, guiding her through two or more courses, and finally releasing her.

F. sanguinea, upon being released from the imposed route, was able to set out for the nest almost at once, and in a fairly straight course, thus completing the remaining side of a triangle or of a polygon, according to the conditions of the experiment. Blinded ants (*F. sanguinea*) and individuals of a poorly visioned species (*Myrmica laevinodis*) could not pass to the nest, but wandered about after being released from the constrained passage.

In Brun's opinion, the ability to pass directly to the nest after being released, in the "Zwangslauf" experiment, depends upon the "ecphorizing of visual engrams, with which the position of the nest has been associated." It cannot be a matter of "local place-memory" nor of "kinaesthetic stretch- or angle-engram," for if that assumption be made, how are we to account for the failure of the blinded and the poorly visioned ants?

In a later paper (1916) two "spontaner Einzelreisen" (*F. rufa*, *F. sanguinea*) were reported by Brun as directly related to the above question.

Each journey lasted for more than an hour, during which the sun's

rays changed sufficiently in angle to seriously disorient the ants, had their orientation been principally upon that basis. These were apparently "Forschungsreisen," since each turn in the course involved a circuitous moving about before the next linear progress was begun.

In one case, there were three successive changes in direction, after which the *rufa* set out straight from the garden wall, across the currant patch and the sand-place to the nest, several meters behind which stood a large fir tree. The latter was believed to have been the reference object. (Cornetz's records contain plottings of many such polygonal courses.)

Instances such as the above suggest to Brun ability to orient with reference to nearby objects, and depend upon the probability that

"bei diesen relativ weitsichtigen Arten, deren Orientierung eine vorwiegend visuelle ist, eine solche Gewohnheit, im Verirrungsfalle hochgelegene Punkte mit freier "Aussicht" aufzusuchen, im Laufe der Stammesentwicklung instinktiv zur Ausbildung gekommen wäre,— etwa in ähnlicher Weise, wie das bekannte "Vorspiel" der Orientierungsflug der Bienen."

It is apparent, then, that the results of the "Zwangslauf" experiment are to be explained by assuming the principal control of movements to be visual in nature, and the influence of the kinaesthetic factor essentially secondary. However, two other experiments conducted by Brun (1914, 1916) show that if circumstances permit, the proprioceptive guidance of orienting movements may be the predominant influence.

In the earlier experiment (1914), a path (*F. rufa*) was established between the nest and a food-place on the opposite side of the experimental table. During habituation the table was tilted (through angles of 20°–45°) toward the nest or toward the food-place, and after formation of the path the direction of incline was reversed. Most of the experiments were conducted under bipolar illumination, and the influence of unipolar illumination was investigated, as a control.

With bipolar illumination the reversal of an inclination of 20° was sufficient to disturb the ants, but under unipolar illumination the reversed angle must be as great as 35° in order to produce disorientation.

This shows that when visual differences exist, the importance of the "kinaesthetic engram" is decreased, but that this factor 'alone suffices for reorientation when all remaining possibilities have been excluded.' Hence "the inclination-angle is a subordinate engram, which may come into relationship with the others, but not overweigh them."

These results explain the ability of ants to make use of elevations and depressions of the terrain in their field orientation. Not only this, but kinaesthetic control may be utilized in passing over level ground (detours around stones, etc.), as is shown by a further experiment (1916).

A bridge of smooth paper led across the experimental table to a larva-place (bipolar illumination), but this time the path was complicated by two lateral deviations, each one beginning four centimeters from the center of the bridge.

In the first experiments, the detours were arranged to lead to the same side. After the ants had carried larvae over the bridge for some time, Brun transferred the larvae to the center of the path, between the detours ("Larvenabholen" experiment,—p. 13), and counted the reactions of the first 100 ants coming to this place from the nest. Eighty of these ants went to the nest with larvae, many of these individuals turning back toward the nest after reaching the 'false' arm (further from the nest); and twenty passed to the former larva-place without turning toward the nest.

As a control, the experiment was repeated with the two detours arranged to lead in opposite directions from the path. Under these conditions, as many ants were seen to go ("incorrectly") the entire way to the platform, after picking up larvae, as went to the nest.

From these results, the experimenter concluded that the ants had ". . . die ziemlich komplizierende kinästhetische Sukzession des Hinweges N-M (Nest to Center), bzw. die Reversion dieser Sukzession, engraphiert."

In our discussion of the experiments that have been performed by the European investigators, notably the Swiss and French, who have been the more active students of the subject, we have endeavored to point out the transition in attitude that has occurred, especially within the past twenty-five years. It is not expedient to attempt an epitome of the present state of

affairs, beyond our discussion of the work of Brun, who appears to have the most comprehensive experimental and theoretical grasp of the problem. It can be said that, as time has progressed, attitudes toward the function of the sense organs in orientation have greatly broadened. Although at first the emphasis was placed upon olfaction and the odor trail, the minor rôle of this factor in species that later came under investigation led attention to other possibilities, notably to vision. The importance of the kinaesthetic factor has also been taken more adequately into account, although there has been some misunderstanding of its function, e.g., the "sense of angles." In particular, the recognition of inter-species differences has been very valuable, and is mainly responsible for the more recent tendency to consider the variation of the factorial influences, in the case of any one species, according to the circumstances of orientation.

The shortcomings in the European contributions lie in the fact that in general they are based upon a conception of ant orientation which is too static. Few investigators display a comprehension of orientation as a growing process, involving individuals that learn throughout life. Such an attitude is quite necessary, and the American investigators (Fielde, 1901-1907, Turner, 1906-1913, and Shepard, 1910-1914) have contributed much toward its development.

Fielde studied the behavior of ants (*Stenamma fulvum piceum*) forced to learn their way through an apparatus in carrying larvae and pupae to the nest. Her important contribution was the suggestion of a technique whereby the out and in trails of ants could be studied. Although it had flaws in technique, her work conclusively demonstrated the necessity of considering the individual ant as a separate problem to be studied before attempting to draw conclusions from observations of mass behavior, a point emphasized by Cornetz shortly thereafter. Fielde's strongest proof of this was the failure to find any evidence that an ant, in establishing her own path, could be aided in any way by other ants.

Fielde's apparatus was composed of a series of four open square pathways, concentrically arranged and set off by walls of cemented glass

strips. All of the alleys opened into one diagonal alley which ran from the nest to the opposite corner of the apparatus, where pupae and larvae were placed, in the experiments. The situation thus involved no culs-de-sac; only four pairs of L-shaped detours opening into the common diagonal pathway.

To start an experiment, pupae were placed in the corner opposite the nest. Then marked (temporarily marked, with water colors) and unmarked workers from the nest were "introduced" to this corner, and allowed to find their way to the nest. After a homegoing random journey without a burden, some of the ants returned for pupae. Leaving the pupa-corner, many of these ants would make several ventures into the alleys, going further each time, until at last the nest was reached. On further trips, if an ant passed through more than one alley, she would take one previously covered by herself, regardless of the course followed by the other ants. Fielde noticed no tendency for the shortest run to be most frequently taken, although no burden-bearing ant was seen to loop in her own trail.

Each individual ant was found to establish her own trail, quite independently of the trails taken by the other ants, and to follow this path through the majority of trips. One ant was able to establish a new path when the established one was blocked, but returned to it when the block was removed. No essential relationship was observed between the outgoing and ingoing trails,—the ants "appeared to follow the line of least resistance, or to be influenced by convenience."

It was noticed that many ants gained speed in the carrying in of pupae as the number of trips increased. "If there could be no greater stimulus in the greater amount of scent laid down," Fielde reasoned, "the gain in speed must arise from added familiarity with the road." This suggests learning.

Fielde's experiments on the influence of the odor-trail were not well controlled. For example, she stirred up the layer of earth covering the bottom of an alley, through a considerable distance, but the ants were able to cross the area without great disturbance. Nevertheless, it is well to remember that chemical substances which had diffused through the thin layer of earth to the floor of the alley probably would not be effectively altered by displacement of the earth, nor would traces that had diffused to the alley walls.

Turner's experiments were timely, stressing as they did many hitherto unknown but important characteristics of ant behavior.

It will be profitable to pass in review his experimental setting and main results.

The apparatus involved a raised cardboard stage, from one or the other side of which an incline led down to the plane of the nest. At the beginning of an experiment, the ants (*Myrmica punctiventris*, *Tapi-noma sessilis*, or *F. subsericea*) were placed on the stage, with pupae, and made to find their way to the nest, being allowed to return to the stage for further burdens after the first had been deposited in the nest.

When ants were deposited with pupae in this manner, a few individuals began to carry, then others joined them, moving at first "as though feeling their way," but later with more assurance and greater rapidity. After all of the pupae had been removed, the ants were seen to "explore thoroughly both stage and island, and then would gradually withdraw from the stage."

Upon repetition of the experiment for the same group of ants, the time required for the first ant to reach the nest with a pupa was less, and decreased still more for further trials. The time for successive trips made by any one ant (marked temporarily) was also seen to decrease. Hence the first few trials could be definitely contrasted with later trials,—“the slow and exploring gait with which most species make the first few trips of the initial experiment of any series, when contrasted with the rapidity of the later movements, indicates that the ants learn the way home.”

From these experiments Turner concluded that “if ants are guided in the homegoing, neither by tropisms nor by other forms of reflexes, nor by a homing instinct, the probability is that they learn their way home.” Some time curves were presented (1907), to show the shortening tendency that came with subsequent returns to the nest. In their early course, most of these curves are irregular, and display a rapid drop, but their later trend tends to be smoother, and their decline more gradual.

Another notable result obtained by Turner was that “if any complications were introduced the ants were sure to be delayed until they had been mastered.” However, after the trail had been learned from stage to nest, by way of an inclined pathway twelve inches in length, the incline could be turned end-for-end

without disturbing the ants that crossed it.⁸ Yet "the readiness with which ants react to any strange odor that is added to their pathway lends support to the view that the odors of the pathway itself form part of the psychic impression of homegoing ants."

This conclusion was confirmed by the fact that if an ant had been habituated to pass over an incline which included a band saturated with xylol, and this band were later removed, the animal would stop at the place where it had been located. Apparently, "from the ant's standpoint, the transverse band of volatile substance was still on the incline. . . ." It seemed to have "become a familiar part of the homeward path." Turner concluded that it is "not the scent of the trail merely, but the odor peculiarities of the pathway as such, that form a part of the impression which enables ants to pass home."

This principle apparently is also true of tactile stimuli. If a *Myrmica punctata* ant had learned to pass down an incline with a smooth black surface, she would be disturbed by the substitution of a black incline with a velvety surface. However, in similar circumstances, a *F. rufa* was not disturbed.

Turner also found the direction of illumination important in orientation, whether the light came from a window or from a lamp at one side of the apparatus. He performed the following experiment to investigate this problem.

In the experimental situation already described, the ants were allowed to stabilize their pupa-carrying, running down an incline leading from one side of the stage. A light was placed on this side ("at times") during the habituation period. When a *new incline*⁹ could be intro-

⁸ There is little doubt that Brun's experimental contrast between (apolar) larva-trails and (polarized) honey-trails will account for Turner's finding.

⁹ This experiment can be performed to demonstrate virtual orientation to the direction of illumination, but in such a manner as to preclude the hesitation and wandering that occurred when the lamp was shifted in Turner's experiment. If *two* inclines are regularly exchanged in position on the side used during habituation, and if one of these (rather than a new and 'unsaturated' incline) is placed on the other side of the stage, to lead in the opposite direction from the first (kinaesthetic precaution) when the lamp is changed in the test, the ants will pass down the new incline without disturbance. This shows that as Turner performed the experiment, following the change in direction of illumination neither the olfactory nor the kinaesthetic characteristics of the situation were the same as before with respect to the visual. When studying the influence of one orienting factor, the others should remain under control.

duced to the other side of the stage without any of the ants passing down it, the experiment was in order.

The lamp was then moved 180° to the opposite side of the stage. The ants were observed to pass to the side of the stage opposite the originally used incline, hesitate and wander near the new incline (see note 9), and after a considerable time go down this to the nest. Any angular change in position of the lamp brought effects similar to this, but changes in its intensity (4 C. P. to 8, to 16, to 32 C. P.) failed to disturb the ants.

Turner concluded that “. . . the light is responded to as a means to an end, and not as an end in itself,”¹⁰ and in addition that “ants use such things as irregularities in surface, edges of flat surfaces, the edges of shadows,” etc., as reference data. These statements offer further proof of the versatility of his conception of the coöperative relationship that exists among vision, olfaction, and the other utilized factors. For this contribution, and for his emphasis of the learning ability of ants, Turner’s place in the literature should not be a minor one.

Shepard’s experiments (1910–1914), of which a detailed report is soon to be published, carried further the suggestions of Fielde and Turner, and represent the first extensive investigation of insect learning.

The maze used consisted of a system of $\frac{1}{2} \times \frac{1}{2}$ ” alleys cut into a wooden base. In the fundamental pattern of the labyrinth, a long central alley connected the entrance with an expansive food-box, and reached

¹⁰ According to Wheeler, in his discussion of the visual factor, Turner “seems to overlook the fact that it can have only subordinate significance, as many of our ants forage as readily at night or in . . . the holds of ships . . . as they do in the daylight, that many tropical and desert species are nocturnal at certain seasons, and that others are permanently nocturnal or hypogaecic.” This statement seems somewhat unjust, for although it is true that in many species, due to a characteristically unilluminated environment, or to deficiencies in or lack of visual receptors, vision is *permanently subordinated* to other means of orientation, and that in other species vision may be *temporarily subordinated*, because of an ant’s presence in a situation that offers no visual heterogeneities, or because of the forcefulness of the control exerted by other factors at the time, we are not justified in making dogmatic statements as to the general importance of vision in controlling orientation. What is true for one species may not hold for another, and a statement that is in order for the orientation of a species under certain conditions may well fail under other conditions.

the latter by means of two paths leading into it from opposite sides. Passing from the nest end of the central alley, the first complicating features were two rectangular lateral detours, one of these having a smaller square detour at one corner, and a straight blind alley at each corner. Nearer the food-box, on the central path, were two pairs of lateral blind alleys. This section could be rotated, since it was part of a block moving freely in the maze base. Still nearer the food-box on the main path, a series of alleys diverged at angles from one another like the spokes of a wheel, four of these being closed alleys (culs-de-sac), the other three open and leading to the food-box pathways.

By appropriately introducing small blocks to various parts of this maze pattern, many different patterns could be obtained. To control the olfactory situation, the floor and walls of alleys and food-box were covered with pasteboard. Illumination was furnished by a lamp which could be hung in any position with respect to the maze. (The experiments were conducted in a dark-room.)

The maze alleys were numbered for convenience in taking records. On different occasions individual ants were temporarily identified by means of a dash of paint on the gaster, but whenever possible anatomical peculiarities were utilized to enable identification over longer periods of time.

The ants (*F. exsectoides*, *F. subsericea*) were allowed to pass through the above maze in order to get food and to carry it to the nest. From the results obtained in manipulating the pathway linings, Shepard concluded that in the orienting process "olfaction plays a definite part, but not a controlling part," since in many of his studies the ants were found able to master the situation under conditions such that the chemical trail could not have been a guide.

The importance of vision was studied by means of changes that were made in the position of the lamp during and after learning of the maze. After the maze had been learned with the illumination consistently from one side, when the lamp was moved to the opposite side in the course of a maze trip, the ant was seen to stop, wander a little, and then reverse her direction of progress. If the 180° change was made when the ant was not in the maze, she would appear quite disoriented upon her next entrance. Further, an ant that had learned the maze under

constant illumination from one source could be led in many directions through the situation by means of appropriate changes in the position of the lamp (see note 43, p. 110).

Other tests demonstrated the importance of the kinaesthetic or muscle-sense factor. It was found that more rapidly traveling ants that had learned the maze fairly well were able to pass through it successfully under conditions involving complete elimination of the light. Turning the controlling light on and off at intervals seemed no serious disturbance to the rapidly moving ants, although the slower ones appeared to be lost in darkness. Since in these experiments sufficient steps were taken to eliminate the possible influence of the olfactory and visual factors, the effective "cue" must have been kinaesthetic, and furnished by the spatial relationships of the maze alleys.

Shepard concluded that the visual, olfactory, and kinaesthetic factors are effective in that order for the orientation of the species studied.

The two *Formica* species observed by Shepard were found to possess a surprisingly high learning ability. Moreover, "the associations acquired in maze-learning were found to persist for some time, since there was little apparent decrement due to disuse over an interval as long as a week between original learning and the relearning tests.

Van der Heyde (1920) conducted rather simple tests of "le pouvoir d'apprentissage" of *F. rufa*. Two of his three investigations are of some interest for our general subject.

In the first type, the apparatus consisted of a "labyrinthe" (rather, a simple alternation box) with four compartments, for which zinc bands served as walls. The apparatus was covered with glass, and rested upon a sheet of paper which was renewed between trials.¹¹ The ants were transferred with tweezers¹² from the nest to the starting compartment,

¹¹ This was not a complete control of olfaction, since substances could diffuse to the walls, and through the paper to the floor.

¹² The handling with tweezers is not a desirable procedure. From the account given, there was undoubtedly a rather violent emotional response to this in most cases. Perhaps this fact accounts for the failure of many of the ants to learn the simple situation employed.

released there, and allowed to find the way through the alternate openings. One ant was run at a time.

There were marked individual differences in the ability of the ants to learn this situation. One persisted in running excitedly about in the first alley, and other ants shortened their time very slowly, while some did not learn at all.

In a typical case, the ant, when first placed in the apparatus, wandered about for some time in the first compartment, and then passed more quickly from one compartment to the other, as if it had "become familiar with the notion of the opening and had lost its instinctive antipathy for the passages,—that is, that he applied the experience of the first compartments to the others." The experimenter's tracings show that with further trials, as the required time decreased, the movements made in passing from the first to the final compartment tended to be reduced to a minimum.

In a second experiment, a simple T-apparatus was employed, one short arm leading to the nest, the other to a blind end. The apparatus was constructed of cardboard, and the absolute position and rôle of the two arms remained constant throughout the trials. The ants were introduced to the long arm, and in the course of further trips quickly learned to turn directly toward the arm which led to the nest, the total required time shortening fairly rapidly in all cases. It is not surprising that this situation, involving only a simple position habit, failed to be much of a problem for the ants.

C. Apparatus and methods

1. *The general situation; the ants and their nest life.* Under natural conditions, the workers of most species of ants leave their nest, forage at a distance, and return with food. It is our problem to study the change that is to be observed in the behavior of the individual forager as her experience in the situation increases. Investigating the question in the laboratory (for control purposes), it is highly desirable that the experimental setting approximate the natural environment as closely as possible.

To this end the experiments discussed in this paper, after

Shepard's method, employed the food-foraging habit, necessitating a journey through the maze in order to obtain food, and a return through the same maze (in reverse order) to regain the nest.¹³ This food-carrying must be a part of the normal nest routine, in which the experimenter does not intrude except to

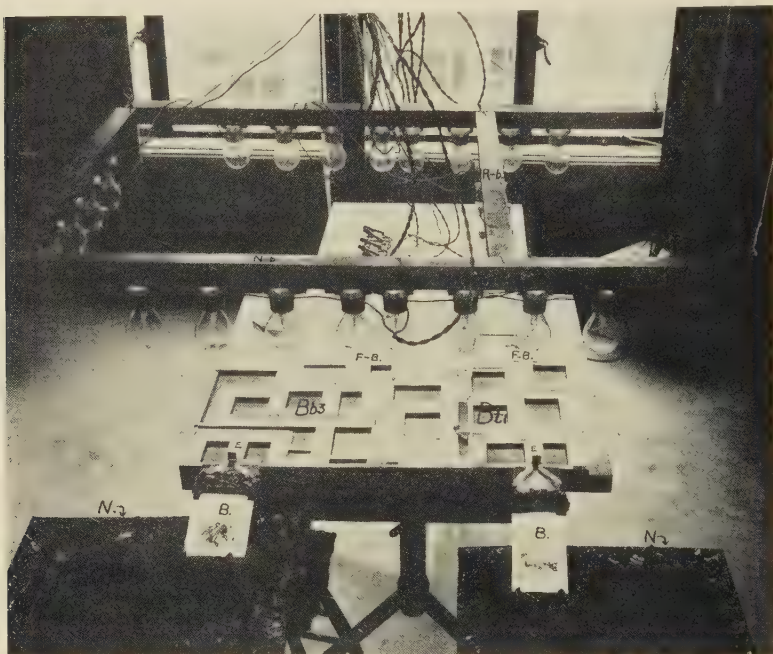


FIG. 1. THE EXPERIMENTAL SETTING (SKY-LIGHTS AND DARK SHUTTERS OPEN)

B, bridge from nest to maze; *E*, entrance alley; *F-B*, food-box of maze; *N*, nests; *Bb3*, *Dt1*, mazes in use; illumination for maze *Bb3*: *N-b*, nest battery; *R-b*, right battery; *L-b*, left battery; *F-b*, food-box battery.

allow entrance through the maze at suitable intervals; and the nest life must be free from disturbance. To keep ants in the laboratory over considerable periods of time, in healthy condition, without interfering with the routine and special activities characteristic of life in the open, is indeed a problem.

¹³ The trip from the nest to the food-place, and the return to the nest, may be forced through different situations. The writer has employed this method in later experiments.

The major portion of the investigation was conducted with two species of *Formica*.¹⁴ The ants were taken from their field nests at the Forestry Farm west of Ann Arbor, and were allowed to establish themselves in the laboratory. There was one large 'home nest' for each of the species, and for the experimental work branch colonies were established in smaller 'maze nests.' As occasion demanded, workers were taken from a home nest, marked, and placed in one of the maze nests. When not in use, these nests were wheeled to another part of the laboratory, and into direct sunlight, unfiltered by glass, whenever possible.

The moisture of the nests was carefully controlled by regularly sprinkling the larger part of the top earth with determined quantities of water. The home nests were supplied with a balanced ration of honey or jelly, butter, egg white, and insects or raw beef. For the maze nests, foods that the ants could lap but could not carry away in their mandibles (jelly or honey, and occasionally egg white and butter) were placed on the lower platform of the maze bridge.¹⁵ The ants could obtain the finely cut raw beef, their protein, only from the food-box of the maze.

(It has proved most satisfactory, from the standpoint of obtaining the greatest number of maze trips under constant conditions, to use raw beef cut into very small pieces and allowed to dry before being placed in the food-box. For many reasons, it is undesirable to employ larva-carrying in a study of learning. An ant carrying a small piece of meat can run without impediment, but an ant carrying a bulky cocoon or larva must make many irregular movements in passing through the alleys with the burden, thus unduly complicating her orientation.

¹⁴ The species were *Formica fusca* L. var. *subsericea* Say,—worker 4-6 mm. in length; body slightly shining black, with faint metallic luster; sparse and short but erect hairs, and longer and denser pubescence; a rather rapidly moving ant,—and *Formica exsectoides exsectoides* Forel,—worker 4.5-8 mm. in length; characteristic deeply excised head on posterior aspect; rather long legs, but withal a slower traveller than *F. subsericea*; mandibles, legs, and dorsal thorax light brown, and gaster dark brown, with blunt scattered hairs. (Description adapted from Wheeler.)

(The writer is indebted to Mr. F. N. Gaige, chief entomologist of the University of Michigan Museum, for the identification of these species.)

¹⁵ When a new group of marked ants was introduced into a maze nest, they soon acquired the habit of going to the block to lap the food, and this increased the probability of their entering the maze when it was opened.

2. *The nests.* The ants were housed in carefully calked boxes, which were mounted on stout legs provided with rubber-tired wheels.¹⁶ Each box was approximately eighteen inches square and deep, and was filled with earth taken from the original nest in the open. Around the top of the nest was a trough ($4\frac{1}{2}$ " wide) containing axle grease. Into one of the upper corners, rising somewhat above the level of the trough, a block was fastened, to serve as landing stage for the bridge which led to the maze.

There were two types, 'maze nests' and 'home nests,' the former a smaller type which could be readily moved about. All of the nests were planted with original colonies, those for the home nests each containing about 1,000 workers and five or six queens, while the average maze nest colony numbered two or three hundred workers and two queens. The ants, brought into the laboratory after having been taken from their nest in the open, were placed on the surface of the earth-filled artificial nest with their larvae and pupae, and allowed to establish themselves.

When in use, each maze nest was connected with the maze by a bridge, which led from the corner block of the nest to the maze entrance. From the block, the first unit of the bridge, an upward incline of about 20° , led to a platform which was level with the floor of the maze. (The bridge platform was covered with a removable piece of bristol board.) The maze end of the bridge platform tapered down to a fitted zinc trough which could be slipped under the bristol board lining of the maze entrance, thus tightly connecting maze and bridge. A piece of zinc, sliding down into a slot between the bridge and the entrance alley, controlled entrance to the maze.

3. *The mazes.* To permit facile changes in the partial or entire pattern of a maze, some type of 'universal' system was necessary. That finally chosen was constructed on a base of seasoned maple, 40 inches by 40 inches by $1\frac{3}{4}$ inches, which was composed of many closely jointed pieces secured on the bottom by two L-braces. The surface of this maze base was plotted off into $\frac{15}{16}$ inch squares, and holes were bored at the intersections to receive the pins by which the alley walls were to be attached to the base.

¹⁶ For early experiments (1924-'25—on 'communication,' dropping of objects from heights, etc.) conducted on large trough-enclosed tables, tall metal (earth-filled) nests were used. The side entrance of each nest, a series of horizontally arranged holes, allowed the ants to reach the table by passing down a long plaster-board incline.

Wooden strips $\frac{1}{2}$ inch high by $\frac{3}{8}$ inch in width were used for alley walls, in order to furnish a surface upon which the glass alley covers could rest. Each alley wall strip was pierced on both ends by countersunk pins, which fitted into the holes provided for them in the base. Hence the alley walls could be readily changed in position when desired. (The securing pins were $\frac{1}{16}$ inch in D; the alley wall strips $\frac{3}{8}$ inch in width by $\frac{1}{2}$ inch in height, and cut in length according to the maze pattern.) The standard alley width was $\frac{3}{4}$ inch, for any pattern.

The walls of the maze alleys were topped with narrow strips of white felt, not permanently fastened, in order to permit changes in position for control purposes. All of the alleys were covered with plate glass pieces $\frac{1}{4}$ inch in thickness, which were edge-ground to permit close fitting. The entire system was quite 'ant-tight.'

The bridge, all alleys of the maze, and the food-box, were lined with units of thin tough bristol board, which covered the bottom and walls. These pieces were cut to fit closely together, and to leave no slit between two turned up edges or between two adjacent linings. The lining units were of a standard width, and hence readily interchangeable when cut for alleys of equal length. To facilitate performance of the 'exchange routine' (see pp. 36 and 43), conjoining blind alley and true path units were supplied with a lining cut in one piece.

With this system, it was possible to make maze patterns of any complexity desired. The patterns Bt1 and Bb1 (figs. 1 and 2), used in most of these experiments, were mounted on the same base, to permit using a common system of illumination.

4. *The lighting apparatus.* Throughout the experiments it was necessary to control the visual situation by illuminating a maze from any one of the four principal directions, or by combining two or more of the four sources. This was made possible by the apparatus shown in figures 1 and 2, and described below.

The illuminating apparatus for mazes Bb and Bt involved three shorter transverse bars ($1\frac{3}{8}$ " sq.), each bearing a 'battery' of four 110 V., 20 W., clear ('mill type') Mazda lamps; and two longitudinal bars,

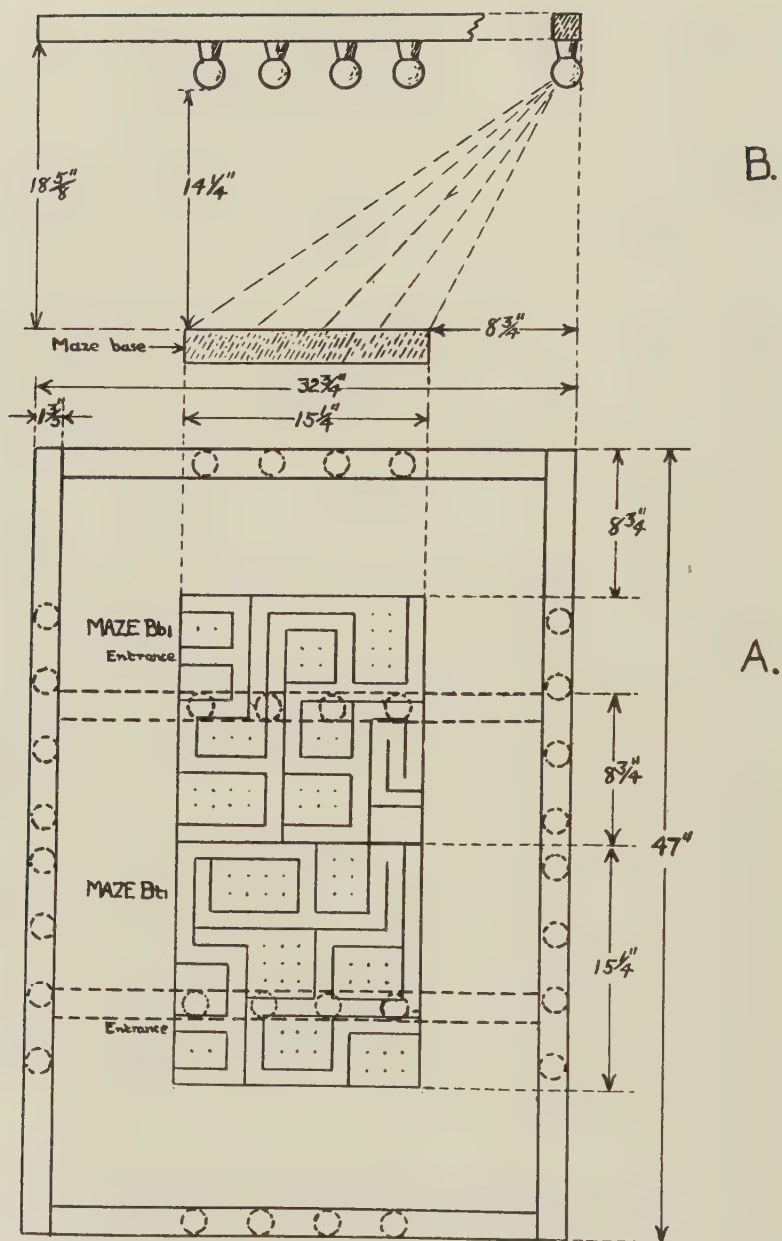


FIG. 2. A, MAZES, LIGHT APPARATUS, FROM ABOVE; B, MAZES, LIGHT APPARATUS, LATERAL ASPECT

each with two batteries of four lamps each,¹⁷ arranged as shown in Figure 2. This apparatus was suspended over the Bb-Bt base, making it possible to illuminate either maze symmetrically from the four sides by moving the center transverse bar to the appropriate position.

The angular position of the light batteries with respect to the surface of the maze was adjusted to insure the illumination of each alley, with a minimum of shadow. To approximate uniform intensity of illumination along a line in the maze parallel to the illuminating source, the bulbs of each battery were equidistant from one another, the two outer bulbs being even with the sides of the maze. A control board enabled using the batteries singly or in combination.

5. *The labelling of 'record ants.'* The great impediment to studying the behavior of an individual ant over a considerable period of time has been the difficulty of labelling the ants in a distinctive and relatively permanent manner. Observers have either contented themselves with studying mass behavior under different conditions, or have marked ants for short periods with such temporary traces as a dash of paint on the abdomen. Shepard, in his maze studies, also made use of anatomical peculiarities to identify individuals.

For the present experiments, the desideratum was a mark that could be applied by the experimenter as new record ants were needed, and one that would adhere over a long period of record taking, without necessitating the emotional disturbance occasioned by renewal. The moisture and contact incident to nest life remove any artificial mark in a very short time, unless the mark is a particularly tenacious one. Readily recognizable anatomical peculiarities are useful, but not always at hand when needed, and this method of identification often leads to confusion; while imposition of such features by clipping of legs and of antennae renders an abnormal animal whose records can mean little for a study of normal orientation. A mark, then, must permit facile identification, must not interfere with the movements of the animal, and must not drop off easily. To meet these requirements, the following method

¹⁷ As an ant moves along on one side of a single lamp, there must be a considerable variation in the stimulation of the compound eye facets for different points in her course. To remove this difficulty, it would be necessary to place a single source at some distance from the path. This is impracticable; hence our use of lamps in 'batteries.'

of labelling (a thin tissue mark fastened to the dorsal aspect of the gaster, with rubber cement) proved fairly satisfactory.

The ant to be marked was allowed to crawl onto the volar surface of the experimenter's forefinger, gently held in position there with gaster pointing toward the end of the finger, and the label was attached as follows. Over the top of the largest segment a thin layer of light shellac was quickly spread, upon this a thin layer of Buhl's rubber cement, and finally the mark, a thin piece of tissue bearing the symbol, was placed on the rubber cement base and tamped into position. Three teasing needles were used for the successive steps. (Shellac, cement and label must be applied quickly, or the cement will be too dry when the mark is applied. If the operation is performed rapidly enough, the shellac may be dispensed with.)

The labels were so planned as to permit ready distinction among them. Differences in symbol, size, and shape were all employed.

No more than fifteen marked ants were introduced into any maze nest at a time, the usual group containing ten individuals. These ants were taken from the home nest one by one and labelled, and were placed in a Janet-Fielde nest in order that their marks might 'set' before being subjected to the various tests of life in an earth-filled nest. After two days the Janet-Fielde nest was placed on the surface of the maze nest to allow the ants to run out into their permanent home.

6. The taking of records. At the beginning of any series of experiments, the maze nest to be used was connected with the appropriate maze. If a new group of marked ants was introduced at the time, a period of four days was allowed for their habituation to the nest, before the maze observations were begun. During this interval the ants were free to acquire the habit of going to the bridge platform to lap at the jelly or honey placed there.

At the end of the habituation period, the maze observations were begun. Before each experimental period, the light-proof shutters were closed and the appropriate battery of lights illuminated. Fifteen minutes later the jelly was removed from the bridge, the maze door was opened, and the entrance of record ants awaited.¹⁸

¹⁸ For any one nest, the period of experimentation was begun consistently at about the same time of day. It was often found effective, for a new maze nest or

Nearly all of the marked individuals entered the maze at one time or another.¹⁹ All maze entrances of these ants were recorded, but from a single maze nest it was seldom possible to obtain complete records for more than one of the labelled ants.

In recording errors made in the maze, the method in regular use in the University of Michigan animal laboratory was followed. The alleys of the maze were numbered in succession from nest to the food-box, their sub-units receiving a letter designation. Each whole series of true path units (such a series is termed a *situation* throughout this paper) received an odd number appropriate to its position in the maze, and the following blind alley situation received the next even number. Partial progress into any alley or beyond any turn was recorded as a fraction of value relative to the distance covered before the return was made. Separate time and error records were taken for all trips to the food-box as distinct from records for trips through the maze in the other direction. (See note 29 for a description of the arbitrary standard used in error-recording.)

7. Precautions and controls.

(a) *Visual controls.* Large objects in the laboratory, the nests and experimental tables, were painted black, and were below the line of effective vision from the maze alleys. The light apparatus hung directly over the maze, and the battery bars were painted dull black and were all suspended in the same manner, by tautly stretched wires. Controls such as covering the light apparatus with a black cloth, removing the bars, or changing the position of the wires carrying current to the lamps, failed to disturb the ants.

Enclosure of the entire maze and light apparatus within a canopy of black cloth proved impracticable, and other controls were substituted.

for a new group of marked ants, to turn an electric heater onto the nest for a short time before the maze was opened, appropriate steps being taken to prevent the heat from reaching the maze.

¹⁹ The maze-running of unmarked ants was discouraged, when this could be done without disturbing a record ant. Unmarked ants were excluded by the shutting of the maze door, or, if entrance had been gained to the maze, by raising an alley cover to permit escape. The unmarked individuals that proved bothersome by repeatedly coming into the maze were placed in a 'discarded' nest.

The experimenter wore dark clothing during the taking of records, and remained three feet from the maze, frequently moving from one side of the maze to the other or to an end (although when his position was constant during original learning, and reversed afterward, the effect was negative.) The entire maze was often turned through 90° or 180° , but without effect.

To show that the separate lamps of a battery were without influence as orienting features, and to bear out the statement we have made (p. 33) as to the uniformity of illumination for points (within the maze) equidistant from the battery in use, it was found that lateral displacement of a battery by as much as six inches failed to disturb maze-running.

The laboratory walls and ceiling were painted neutral gray, and the mazes were set far enough from them to eliminate the possibility of effective inequalities in reflection.

All changes in direction of illumination which were introduced following original learning,—except for occasional experiments involving changes for the trip to the food-box and others introduced at various points during progress through the maze—were instituted after the ant had reached the food-box, while she was getting a piece of food. Hence, as a control, the trips to the food-box during these experiments were all made under the visual conditions effective during original learning. After the trip to the nest under the changed condition, the illumination was returned to the original direction in preparation for the next trip to the food-box.

(Heat—The batteries were set at a sufficient distance from the maze to eliminate the possibility of heat from the lamps serving as an orienting factor, as many tests with filters adequately demonstrated. To keep the maze alleys at a uniform temperature, the maze was covered with heavy plate glass. The laboratory temperature was under thermostat control.

(b) *Olfactory controls.* Since among the three main factors of possible orienting significance the present studies were directed chiefly to the examination of the visual and the contact-kinaesthetic, steps were taken to reduce the importance of the chemical factor. To this end the single bristol board unit which lined adjacent true path and blind alley was turned end-for end at least once in four trips, at each of the junctions (the *exchange routine*). The pathway linings were always exchanged, in this routine, while the record ant was in the nest depositing the food she had carried. (The glass alley cover was removed and laid on a clean cloth, and the lining was turned with tweezers.) No

alley lining was ever handled except with clean metal tweezers, and rubber gloves were worn when the linings were originally cut and adjusted.

It is possible that chemical traces laid down in the ant's passage through the maze alleys may transfer themselves, through volatilization, to the walls and ceilings of the alleys, in addition to the floor. Diffusion to the walls of alleys was controlled by the routine exchange of linings at the junctions, and to control transfer to ceilings of alleys, each glass cover was turned end-for-end and top-for-bottom at least once every fifteen trips. Under these conditions, there was no disturbance. (However, if the ant were allowed to learn the maze, and the glasses covering adjacent true path—blind alley situations were then exchanged for the first time, some disturbance was evident in most cases.) When turned and reversed, the glass pieces were wiped with a clean cloth. They were also frequently washed in soapless water.

Pieces of meat that were carried into the maze by irregular wanderers, and any particles of earth, pupa cases, or other material carried into the maze from the nest, were at once removed with tweezers.

In every case the maze nest was at least one foot from the maze entrance. The square of cardboard on which the food was placed in the food-box was approximately six inches from the last alley of the maze. Any possibility of either the nest, on the one end, or the food-box on the other, becoming of importance for maze-orientation, was rigidly controlled.

Whenever records were to be taken from a new group of marked ants, the previously used alley linings were removed and new ones substituted throughout the maze. This procedure was effective for all experiments discussed in this paper.

(c) *Contact and kinaesthetic controls.* The maze base did not warp, and occasional testing with a level showed that its surface remained horizontal throughout the experiments.

The turns of the maze alleys were all at true 90° or 180° angles, and the alleys were quite straight. The linings were closely fitted, so that there was no chance of irregular tactile stimulation.

The possibility of disturbance caused by vibrations transmitted to the maze through the floor was controlled as well as possible by laying the maze on felt pads, and by placing pads under the legs of the experimental table. (The table, with a steel base, and adjustable in height, was constructed especially for work with ants.) The normal maze behavior of the ants indicated that this precaution had eliminated all

but the more intense vibrations (from the slamming of doors in rooms near the laboratory, etc.) In all of the experiments care was taken to

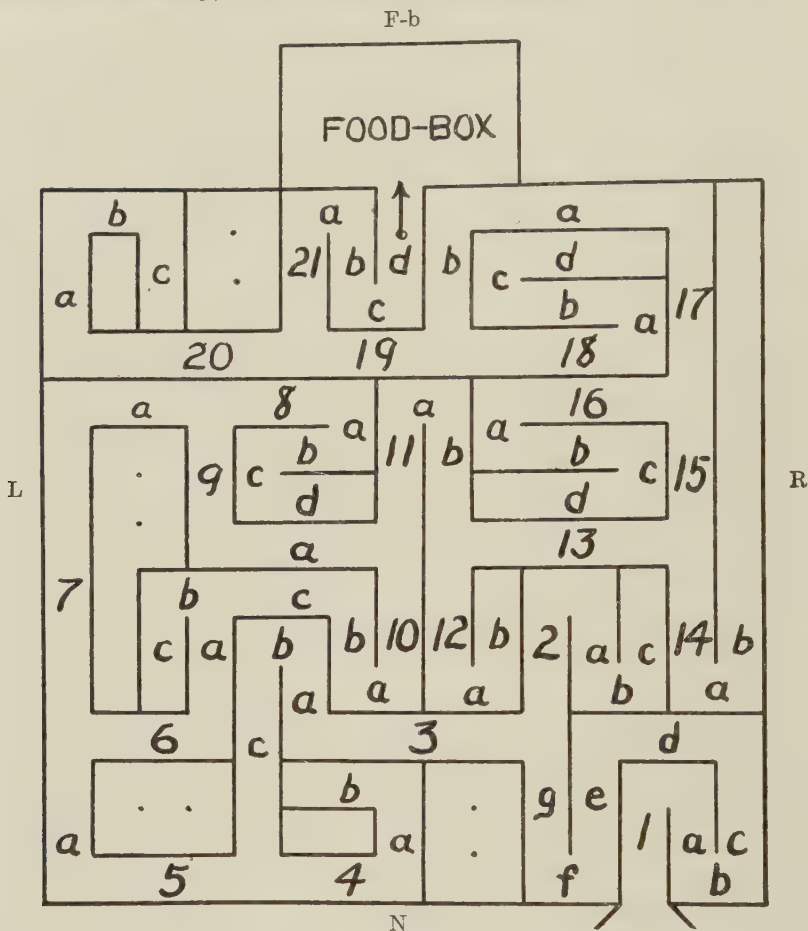


FIG. 3. MAZE A

Designation of directions: *N*, nest side; *R*, right side; *F-b*, food-box side; *L*, left side.

close the maze until such infrequent disturbances had ceased, unless it was desired to study their influence on behavior.

II. EXPERIMENTS AND RESULTS

Introductory experiments were conducted which forced *F. subsericea*, *F. exsectoides*, and *Camponotus pennsylvanicus* indi-

viduals to carry their food through mazes (as maze A, fig. 3) having as many as ten blind alleys. These investigations not only demonstrated how complex a maze situation the ants are able to master, but were also of help in planning the final technique and in designing other patterns for further work.

The maze pattern Bb1 with its modification Bb3 (fig. 4), and pattern Bt1 with its modification Bt2 (fig. 5) were used in the experiments reported in this paper. These patterns were designed to present a moderately difficult test of learning, and to enable close study of the important factors in orientation.²⁰

As we have said, in these experiments it was necessary for the ant under observation to pass from the nest to the food-box (*trip to food-box*) in order to get a piece of food, and to return through the maze in order to reach the nest (*trip to nest*). In treating the results for learning under the various conditions of our experiments, the passages through the maze in the two directions have been taken as separate problems. This will be justified later.

Before the specific objectives of the experiments are discussed, it is considered desirable to treat the possible influence of the chemical factor in maze orientation, in order that our disposal of it may be properly evaluated.

A. *The chemical factor*

The field observations of many European workers have shown that ant species with relatively poorly developed compound eyes depend upon a chemical trail to a considerable extent in their orientation. For such ants, the pathway changes involved in the 'finger experiment' result in disturbance. The generally accepted explanation is that the rubbing of the finger or laying of substances over the path have interrupted the continuity of

²⁰ To permit study of the 'centrifugal swing' factor the Bt1 pattern was designed to 'favor' (see note 30) the true pathway turn at junctions on the trip to food-box, whereas Bb1 was designed to contrast with this in favoring the blind alley turns. For the trip to nest through both of these mazes, the true pathway turn was favored at all of the junctions.

With the exception of alley no. 5 in Bb1 (which could be shortened or lengthened as a check on the contact-kinaesthetic factor), the approaches to junctions were all of the same length for patterns Bb1 and Bt1.

the chemical traces laid down by the ants, of traces that have come to be important for successful orientation on the path.²¹

On the other hand, the experiments of Forel, Fabre, Brun and others (pp. 4, 7, and 14f.) have shown that olfaction is of relatively little importance for genera such as *Formica*, in their field orientation. On the thoroughfares of many species, the finger-experiment produces almost no disturbance. We shall see that the relative importance of the olfactory control in the orientation of the *Formica* species is largely dependent upon the functioning of the remaining factors, and upon the prominence of the chemical stimuli presented by the environment.

1. *Analysis of the chemical trail.* Previous to Bethe's experimentation it had been known that many species of ants 'followed' their own chemical traces, but it remained for him to raise a specific question as to the nature of the process. Bethe's proffered solution, the 'polarization reflex,' was vigorously attacked, but served to arouse general interest in the problem. To supplant this theory, Wasmann offered his 'odor form' theory, and Forel the topochemical theory. According to the latter, the ant perceives the relationship between the shape of objects along the path and their chemical peculiarities, and retraces the path by means of successive arousal of the two, closely associated.

The topochemical theory is suggestive, but there is a lack of satisfactory evidence for it (see p. 13f. and note 7). Brun, who supports the theory (maintaining that when there are objects close to or on the path, the ants may "engraph these in series"), nevertheless agrees with Claparède that it does not explain the results obtained on the flat aphid trails used by Bethe. Part, at least, and probably the most important part, of the guiding olfactory stimuli is based upon whatever substances diffuse from the bodies of the ants as they pass over the path. At any rate, this is the most satisfactory view to adopt in considering the results obtained from experiments involving maze pathways, for

²¹ A considerable amount of attention has been given to Santschi's observation that a *Tapinoma* (*Acantholepis*, *Camponotus*) individual, in passing back from honey to the nest, ("intentionally"—?) leaves a trail of anal gland secretion that probably is of assistance to other ants in passing over the route.

the explanation of which the Forel theory is of no apparent value. It is obvious that olfaction cannot be an orienting factor on a smooth path if there is no part to part difference, quantitative or qualitative. On this point, the existence of some type of 'polarization,' we do not find the literature in complete agreement.

It will be recalled that Lubbock, in rotating a section of *L. niger* larva-trail, found the ants to be disturbed only by conditions which interfered with their virtual orientation to the direction of illumination. When a section of path was turned through 180°, there was no phenomenon of the kind later found by Bethe for the same species on trails to and from an aphid colony (cf. pp. 5 and 6). Bethe's results indicate some end-to-end difference in the nature of the chemical trail; Lubbock's do not. The apparent contradiction has been reconciled in Brun's analysis of his own results.

Brun (1914) observed that when the mid-section of a larva-trail of *L. fuliginosus* was rotated through 180°, there was no disturbance on the part of ants running onto it from either end of the path, whereas the rotation of the mid-section of a honey-trail resulted in the "Bethe phenomenon." Brun explained this by building upon Wasmann's theory, which in turn was adapted from that of Bethe. We may summarize his treatment as follows: 'On the honey-trail there is a two-way polarization, due to the fact that ants coming from the nest lay down an odor predominantly that of the nest, but in amounts gradually decreasing as the honey-place is neared; while ants coming from the honey lay down the honey-odor in amounts gradually decreasing nestward. In contrast, larva-trails are practically apolar, since the same burden is carried through the entire distance, allowing the "heavy larva-odor" to diffuse to the pathway in substantially equal amounts for the entire route, and thus to almost completely cover or neutralize the influence of the "relatively feeble nest-odor."' Hence the results of Lubbock and Bethe are not irreconcilable, since on the aphid-trails (similar to honey-trails) we should expect the ants to make use of the chemical polarization, and thus to be disturbed by an interruption of its continuity,

whereas there is little opportunity for olfaction to become influential on the (practically homogeneous) larva-trails with which Lubbock worked. (In a later paper the writer will endeavor to show that in point of polarization the maze pathway over which dried meat is carried lies somewhere between the above extremes.)

Further, Brun concluded that for "lower" species (*Lasius* species), the "globale Polarisation" of the odor-trail, when present, is effective in guiding the "slavish" passage of the ants over the path; but that for "higher" species (*Formica* species), the "related factors" control orientation, and the ants do not seem to rely greatly upon the odor characteristics of their trails. In respect to this contrast, it is well to remember that the field orientation of most *Lasius* species (*L. niger*, *L. fuliginosus*, etc.) is characteristically a matter of passage along a relatively narrow trail followed by many ants, while individuals of *Formica* species typically pass across an area in a general direction, without their trails being laid upon one another to any extent.²²

A rather different situation exists for the maze-orientation of the *Formica* ants than that which is effective for their field orientation, since in the maze they too must pass along a narrow pathway. Hence facts that hold true for the influence of olfaction in the thoroughfare orientation of these species under natural conditions may not hold for maze conditions.

2. *The 'chemical trail' in maze-orientation.* Shepard's results substantiate our last statement, in showing that unless it is controlled, olfaction is of considerable importance in the maze-learning of *Formica* species. A typical result was obtained when, after an ant had learned the maze, a new pathway lining was introduced to a region in which the trail had not been disturbed during the earlier trips. After running a short distance onto

²² This may be called a *thoroughfare* ("terrain de parcours,"—Cornetz; "Durchgangsstrecke,"—Brun), since it involves the passage of many individuals across an area, and in a general direction, but without any great superimposition of trails. Brun very appropriately terms the narrow path described above a *canalized trail* (a course on which lateral deviation is not likely to occur, due to guiding or restraining topographical features,—e.g., following the side of a wall, or an established chemical trail).

the new pathway the ant was seen to stop rather abruptly, evidently disturbed, retrace her course or wander in the vicinity, and not to cross the new strip for some time. On later trips the difficulty was observed to lessen, and finally to disappear in most cases, when the new lining had been "incorporated as a part of the pathway."

Again, Shepard found that an interesting phenomenon resulted from the exchanging of adjacent true path and blind alley lining units that had remained in their places at a junction throughout original learning. Typically, upon reaching the altered junction and beginning the turn toward the true path alternative, the ant's behavior became excited and irregular. After a considerable amount of wandering, probably including one or more returns along the earlier path, the exchanged lining was hesitatingly crossed. On subsequent trips the disturbance occasioned by the exchange in linings was seen to decrease, and a strong tendency to turn into the blind alley also disappeared. At last, the establishment of the direct turn into true pathway indicated the complete inclusion of the former blind alley lining in the new true path trail.

A related result was that if the adjacent true path and blind-alley lining units were exchanged often enough—i.e., approximately every three trips—the disturbance produced by the exchanges gradually decreased, and finally disappeared.

These and other results indicate that the chemical trail is very effective on maze pathways (*Formica* species), in that it can function as a guiding influence (if undisturbed), at least in determining the direction of turn at junctions of true pathway and blind alley. Whatever the chemical differences (between the alternatives) upon which this discrimination relies, they are very apparently removed from effect by a frequent exchange of the adjacent linings at the junctions (*exchange routine*, p. 36).

The remaining possibility is that the chemical trail may be polarized, and thus serve as a guide for passage through true pathway alleys. On this point Shepard's experiments were negative, in that the turning of a true pathway lining unit through 180° did not affect the behavior of the ants. However, the

writer has exchanged linings from widely separated alleys in true pathway (i.e., the unit from an alley near the food-box for the lining of an alley near the nest), and has found this to produce a slight disturbance in many cases. There is no evidence that this minor polarization can act as an orienting factor. At least, this and other olfactory possibilities were carefully controlled in the present experiments, and the chemical trail (laid down by any one ant in the course of a number of trips) may be regarded as homogeneous, and non-differential at the junctions.

3. *The chemical factor in the field and in maze-orientation.* While Shepard and the writer have found the chemical traces capable of playing an important part in the maze-behavior of the *Formica* species, other experimenters (pp. 4, 7, and 14f.) have reported that in the open these ants are not very dependent upon the chemical characteristics of their paths. The solution lies in the fact that the orienting conditions are rather different in the two cases.

Under natural conditions, the *Formica* species characteristically orient on thoroughfares (see note 22) passing over an area, though in a general direction. Since the paths of the ants are not laid upon one another, the chemical traces of the trips over the terrain are not superimposed to any extent, and hence they are unable to acquire much influence in orientation. However, in learning the maze, an ant passes over the same relatively restricted (canalized) pathway many times, and whatever chemical substances are left²³ become superimposed.

In studying possible olfactory control of orienting responses, then, it is necessary to know whether the ants are passing over a relatively restricted area or over a thoroughfare. Some of the writer's experiments on the harvester ant (*Pogonomyrmex molefaciens*) show these two possibilities in the same situation.

Example: From a large Oklahoma nest of this species several narrow sinuous trails led through the grass toward a rather wide and grass-free

²³ Through contact of the tarsal extremities with the floor; and diffusion of particles from carried food and from the body to the floor, walls and ceilings of the alleys.

footpath. In going from the nest to a grassy foraging area on the other side of the footpath, the ants passed first over a canalized trail, and then over a thoroughfare. On the narrow trails through the grass, scraping off the surface, covering with paper, etc. produced considerable disturbance, although on the wide footpath these changes had no great effect.

Summing up, when there is a chance for the chemical traces to be superimposed, as on the maze pathway or the narrow *molefaciens* path through the grass, olfactory control becomes of considerable importance for orientation. In contrast, the fact that chemical features play but a negligible rôle on the thoroughfares of *Formica* and other genera is apparently due to the lack of summation.

B. Learning and relearning of maze patterns

In observing field orientation, it has been the custom to follow the course of the ant with a corresponding line traced on a record sheet. In general, the tendency of such tracings to become less complicated with time has been taken to indicate ability to 'profit by experience.' However, this fact has received neither proper emphasis nor adequate control.

As we have pointed out, investigators have been interested, primarily, in finding the relative importance of the receptors in the control of orienting movements, and in making inter-species comparisons on this basis. Usually, observations of general behavior are made following an experimental alteration of the situation, and a record is taken of the reactions of the individuals that first enter the changed place. Attention has been called to the fact that under such conditions the experimenter cannot be sure whether any one ant has passed over the path one or many times before the change is introduced. Notwithstanding this, the behavior of all of the ants is usually treated on a common basis.

It is true that the more careful experimenters, such as Brun, make a practice of introducing the experimental alterations only after making sure that most of the passing ants show fairly rapid and regular progress over the path. Usually, in field orientation, such an observation may be taken as an indication that most

of the ants have learned the situation fairly well. Obviously, the reliability of this criterion may vary.

Further, there is every indication that at different stages in the individual ant's mastery of a situation, the receptors do not assume the same relative importance in controlling orientation. To introduce a change (e.g., a visual change²⁴) without knowing at least approximately the degree to which the situation may have been learned by the individuals whose behavior is observed under the altered conditions, is to obtain somewhat equivocal results. This difficulty may have had much to do with many of the wide differences of opinion that are to be found in the literature with reference to relatively fundamental points.

This criticism should be fairly evaluated. The writer does not suggest discarding the valuable general knowledge that has been obtained by means of this method, but rather he proposes that the results be treated with caution. To stabilize the problem of insect orientation, the previous general methods must be balanced with many careful studies of individual behavior over a period of time.

We have reviewed the investigations that have dealt more specifically with the ability of ants to learn (Section IB). Turner agreed with Fielde in finding the ants able to "retain, for a while at least, what they have acquired." His elementary experiments on the maze-learning of cockroaches (1913) impressed the need for further studies of insect learning. Shepard outlined and used a technique that permitted much more detailed study of the problem. He found that the two species of *Formica* investigated by him were able to learn fairly complex maze patterns, and that "the definite associations involved in original learning may be retained at least a week, and on repetition suffer little decrement due to disuse." In the meantime, although the European

²⁴ For instance, a reversal in the direction of illumination is not likely to disturb an ant if she has had limited experience in the situation. In Santschi's experiment, it was found that the reflected light caused merely a hesitation on the part of *unladen* ants, but no turning, whereas the *laden* ants retraced the trail, after turning. Perhaps this difference in behavior is explained by the writer's observation that an ant seldom carries food over a path (at least through the entire distance) during the early stages of learning.

observers (with the exception of Van der Heyde) have not directly investigated the problem, their studies may be taken as demonstrating the many ways in which ants, in their daily activities, show a relatively high learning ability.

1. *Experimentation and results.* The present learning studies were begun with maze A, the pattern of which is shown in figure 3. Although this pattern was fairly complicated, involving ten blind alleys, nine *F. subsericea* individuals were able to learn it during the period of its use (i.e., records were obtained for these ants, although many others also learned the maze).

The main portion of the studies was conducted with maze patterns Bt1 and Bb1 (figs. 4 and 5), using *F. subsericea* and *F. exsectoides* individuals as subjects. Since Shepard previously studied the general features of ant learning, we shall present only a brief account of them, with a case report to illustrate maze behavior over a considerable period of time, confining our detailed study to the mechanics of maze learning.

a. *Behavior of ants in the maze.* An ant placed in the maze for the first time displays evident emotional excitement.²⁵ It runs about on walls and ceilings of the alleys, making many retraceals (returns, back-trackings) in open true pathway or in blind alleys, from one arm to another, and in the end may leave the maze without reaching the food-box. If this random behavior (but not entirely 'random,' as will be seen) takes the ant to the food-box, the process is repeated before the nest is reached. After food has been carried back to the nest through the maze²⁶ the behavior becomes less erratic, although from the first trip there is a decrease in the tendency to run on walls and ceilings of the alleys, and the returns in true pathway and in culs-de-sac are less frequent. The difficulty in making 90° and 180° turns,

²⁵ This excitement is less noticeable if the ant has already learned a maze pattern. For this reason, in later experiments it has proved desirable to allow the ants to run through a simple two-armed passage to a supply of honey, as a preliminary to learning the maze.

²⁶ It is an interesting and important fact that food may not be carried on the first trips to the nest from the food-box, and that even on later trips the ant may reach the nest unladen, having dropped her food in some maze alley.

which at first led to many long and short returns in true pathway and in culs-de-sac, also begins to decrease. With further trips the running is more constant in speed, and is confined more completely to the floors of alleys.²⁷

On early trips the passage from food-box to nest is usually marked by many successive returns to the food-box from parts of the maze, before the nest is reached. This tendency falls off rapidly, and usually disappears before the fifth trip. For example

In the case of ant *m*, *F. exsectoides* (maze *Bt1*), there were thirty-four successive returns to the food-box (an unusually large number) before the nest was reached on the first trip, but less than one-third that number for the second trip, two each for the third and fourth trips, and none for the fifth.

This 'return to food-box' behavior is somewhat more characteristic of *F. exsectoides* than of *F. subsericea* (and in both cases outstanding individual differences are seen). It should also be said that on early trips there is a corresponding tendency, evidenced on the trips from nest to food-box, to return repeatedly to the first alleys of the maze, to the bridge, or to the nest.

With further maze trips, as we have said, the behavior of the animal usually changes rather markedly. The sporadic and irregular errors which we have described briefly above are seen to drop out fairly rapidly, leaving those which for various reasons are more firmly fixed, and which are eliminated only as the result of the conditioning effects of many maze trips (see pp. 56-62).

b. Curves representing progress in maze-learning. (1) *General samples.* The curves shown in figure 6, A, present time and error records for seventy-two consecutive trips, forty-eight of them given to the learning of pattern *Bt1* and the remainder to the mastery of *Bt2*. The following important features may be

²⁷ On this point there are outstanding species differences. *F. exsectoides* individuals are very persistent in the wall- and ceiling-crawling, and especially in the former. *C. pennsylvanicus*, the carpenter ant, clings tenaciously to the habit of crawling upside-down on the glass covers of alleys. In advanced stages of learning, *F. subsericea* confines its passage entirely to the floor.

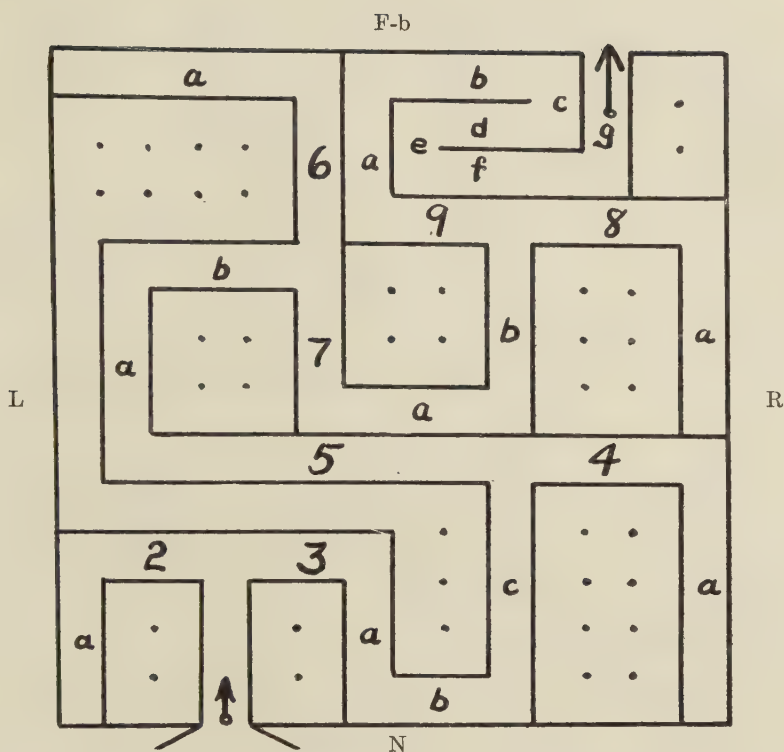


FIG. 4. MAZE PATTERN Bb1

Designation of directions: *N*, nest side; *R*, right side; *F*, food-box side; *L*, left side.

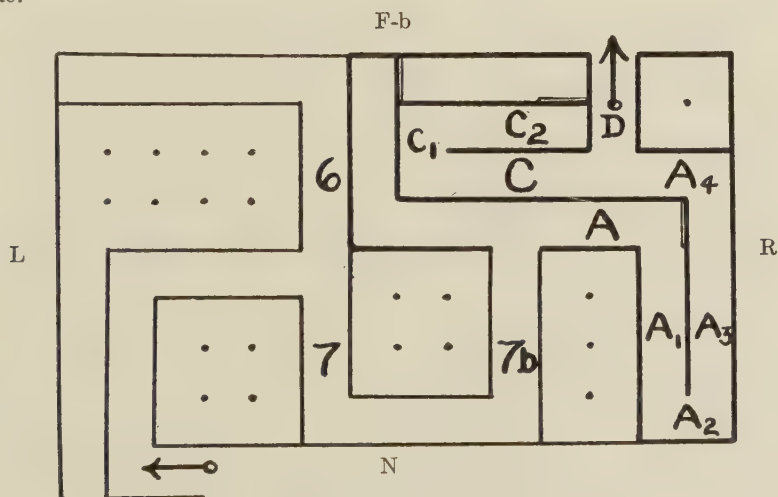


FIG. 4A. MAZE Bb3 (MODIFICATION OF Bb1)

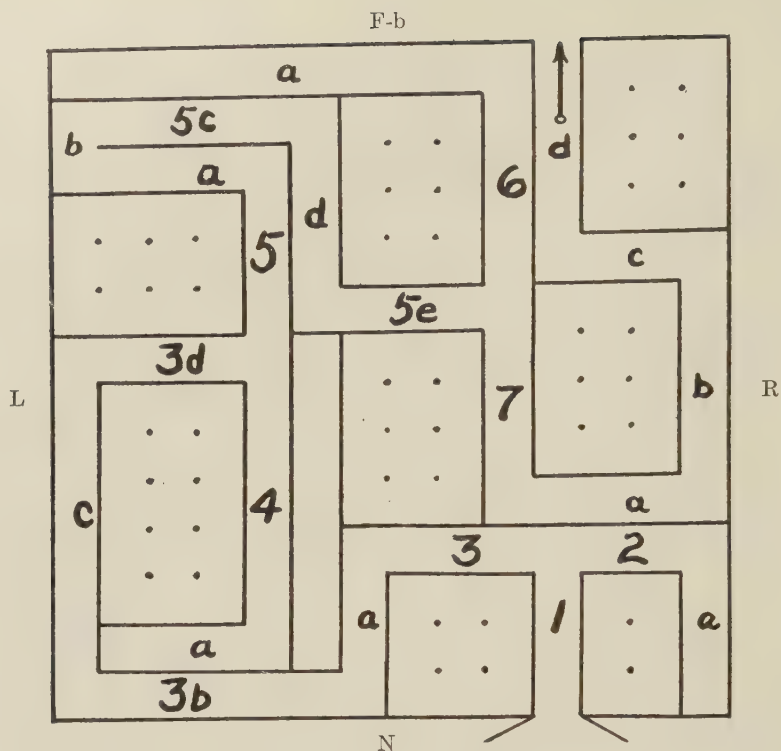


FIG. 5. MAZE PATTERN Bt1

Designation of directions: *N*, nest side; *R*, right side; *F*, food-box side; *L*, left side.

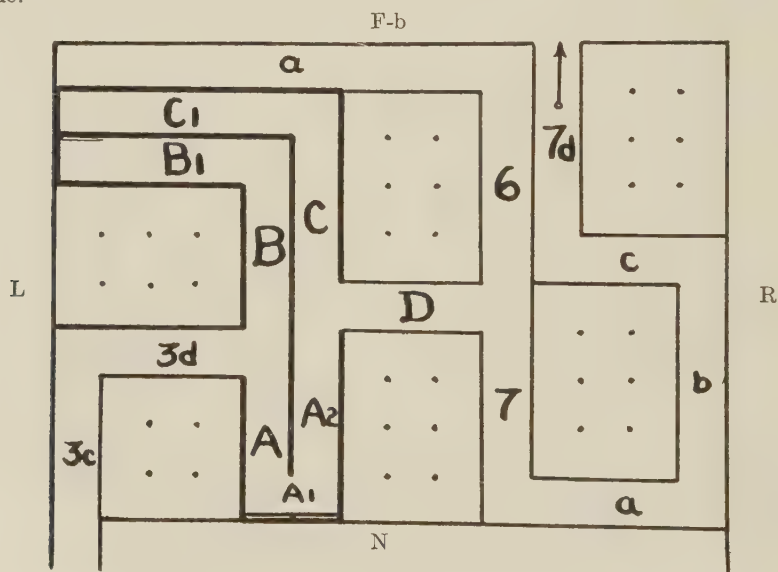


FIG. 5A. MAZE Bt2 (MODIFICATION OF Bt1)

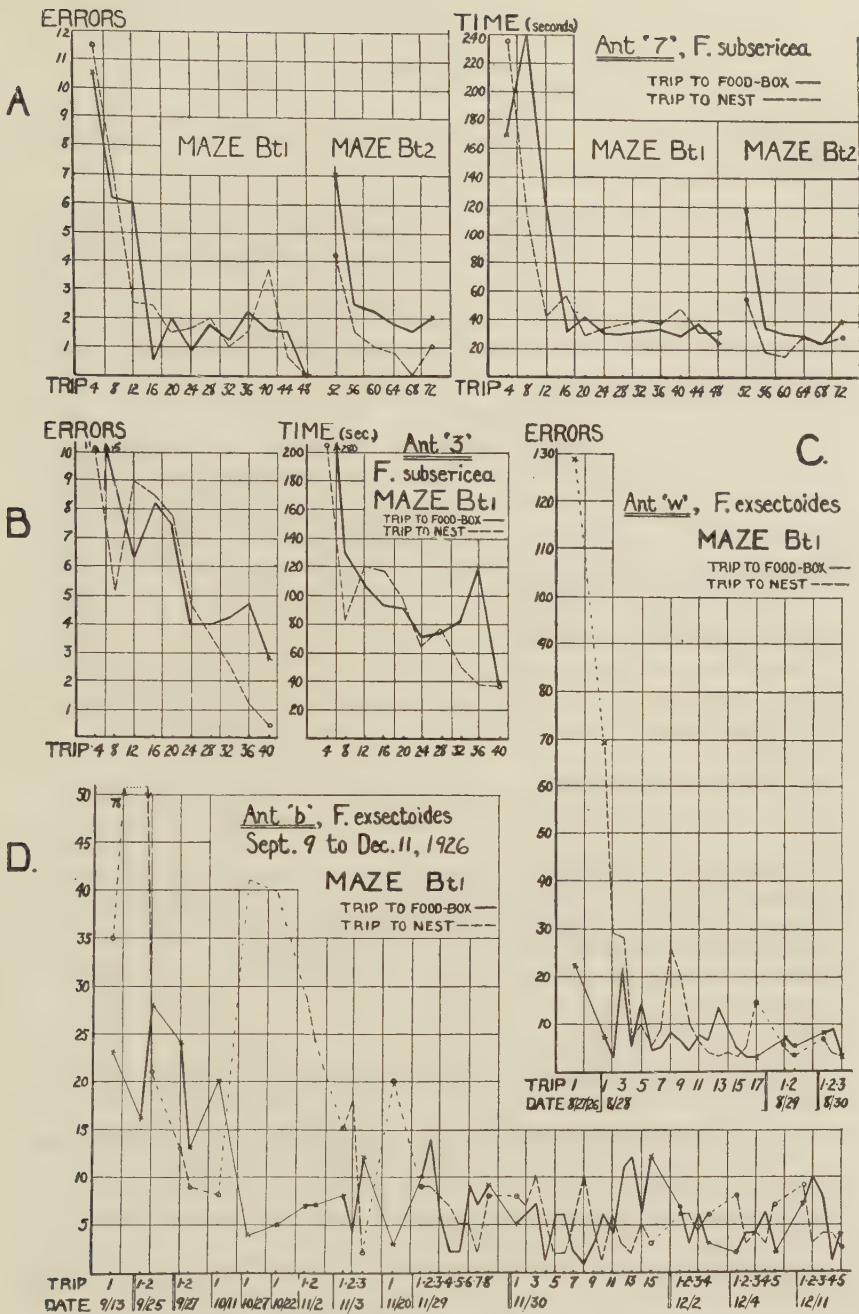


FIG. 6. SIMPLE LEARNING CURVES
Trip to food-box, —; trip to nest - - -

emphasized, since they characterize all curves for ant maze-learning.^{28,29}

a) *The rather close similarity between time and error curves.* Of the two, the time curves seem to be less reliable as indicators of progress in learning.

b) *The initial drop*, characterizing the curves for progress in the two directions (trip to food-box, and trip to nest), and occurring at about the same rate in both cases.

c) *The period of gradual improvement*, following the rapid decline, marks the entire progress as one of the 'negatively accelerated' type. This may be seen from the 16th to the 48th trip in figure 6, A.

d) *The 'intertwining' of the curves* for trip to food-box and for trip to nest, indicating a common degree of difficulty (for this maze), but *not* a close relation in the manner of learning the two runs.

e) *The important difference between the error curves for learning of pattern Bt1 and those for pattern Bb1* (figs. 6 and 7). For the learning of Bb1, the *trip to nest* curve uniformly follows a lower course than does that for the *trip to food-box*. This difference is due to the presence of three 'coerced errors' in the run to the food-box (see p. 56).

As further illustration, we shall briefly consider a few curves selected to illustrate other features often found in ant learning.

²⁸ It should be remembered that the *exchange routine* (p. 36) was effective for all of these experiments. Hence, during the elimination of dependence upon chemical differences, the progress in learning was less rapid. Curves for ant learning drop more abruptly if the trail is not interfered with.

²⁹ The *error curves* have been plotted on the basis of the following method of counting errors:

An error consists in

- a) An entrance to a blind alley;
- b) A retracal in a blind alley (roughly, through a distance of an inch or more);
and
- c) A retracal in true pathway, counting an additional error for each true path-blind alley junction passed in the backward direction.

Additional rules:

- a) All errors made preceding entrance to the food-box are counted in the *trip to food-box* total.
- b) After once reaching the food-box, all errors made in maze alleys before the nest is again reached are counted in the *trip to nest* total.
- c) 'a' and 'b' are plotted as separate curves.
- d) The *trip to food-box* time is that time elapsing between entrance to the maze and arrival in the food-box; the *trip to nest* time is that elapsing between the first exit from the food-box and exit from the maze.

Figure 6, B. Ant '3', *F. subsericea*, learning maze Bt1. Note that the curves for progress in the two directions are very similar in the course they take. The rise in the error curves, following the 12th trip, is due to the disturbance produced by the sudden hard slamming of a door in a nearby laboratory while the ant was on the way to the nest (trip 12). The excitement persisted for some times and its effects may also be seen in the trip to food-box record. The time curves do not show this effect to a great extent, due to the fact that although the ant was making more errors than before, her emotional excitement caused her to move much more rapidly.

Figure 6, C. Ant 'w', *F. exsectoides*, learning maze Bt1. Note the height of the first part of the *trip to nest* curve. This feature is explained by the fact that ant 'w' showed, in a rather exaggerated form, the tendency to return repeatedly to the food-box, on early trips, before passing through the maze to the nest. This behavior soon disappeared, as follows:

August 27, 1926, Trip 1.....	54 returns
August 28, 1926, Trip 1.....	27 returns
August 28, 1926, Trip 2.....	7 returns
August 28, 1926, Trip 3.....	4 returns
August 28, 1926, Trip 4.....	1 return
August 28, 1926, Trip 5.....	0 return

Figure 6, D. Ant 'b', *F. exsectoides*, learning maze Bt1. This ant serves as our example of the individuals that learned a pattern in the course of a few repetitions daily over a considerable period of time. The *F. exsectoides* individuals were more likely to learn in this manner than were *F. subsericea* ants.

Ant 'b' was rather large and clumsy, and hence made errors that the more quickly moving ants did not commit, and failed to eliminate errors that the more rapid travellers and quicker learners succeeded in dropping (i.e., 'b' had difficulty in properly making the turns, and often over-ran into blind alley when the entrance to true pathway involved a 90° turn).

(2) *A sample of learning and relearning extending over a considerable period of time (fig. 7 and Appendix I).* As an example of the cases in which the maze-running of an individual ant was under observation at intervals during a long period of time, the record of ant 'z,' *F. subsericea*, is given. This individual was labelled on December 28, 1926, and on record in maze Bb1 (and Bb3) from January 17 to May 5, 1927.

ERRORS

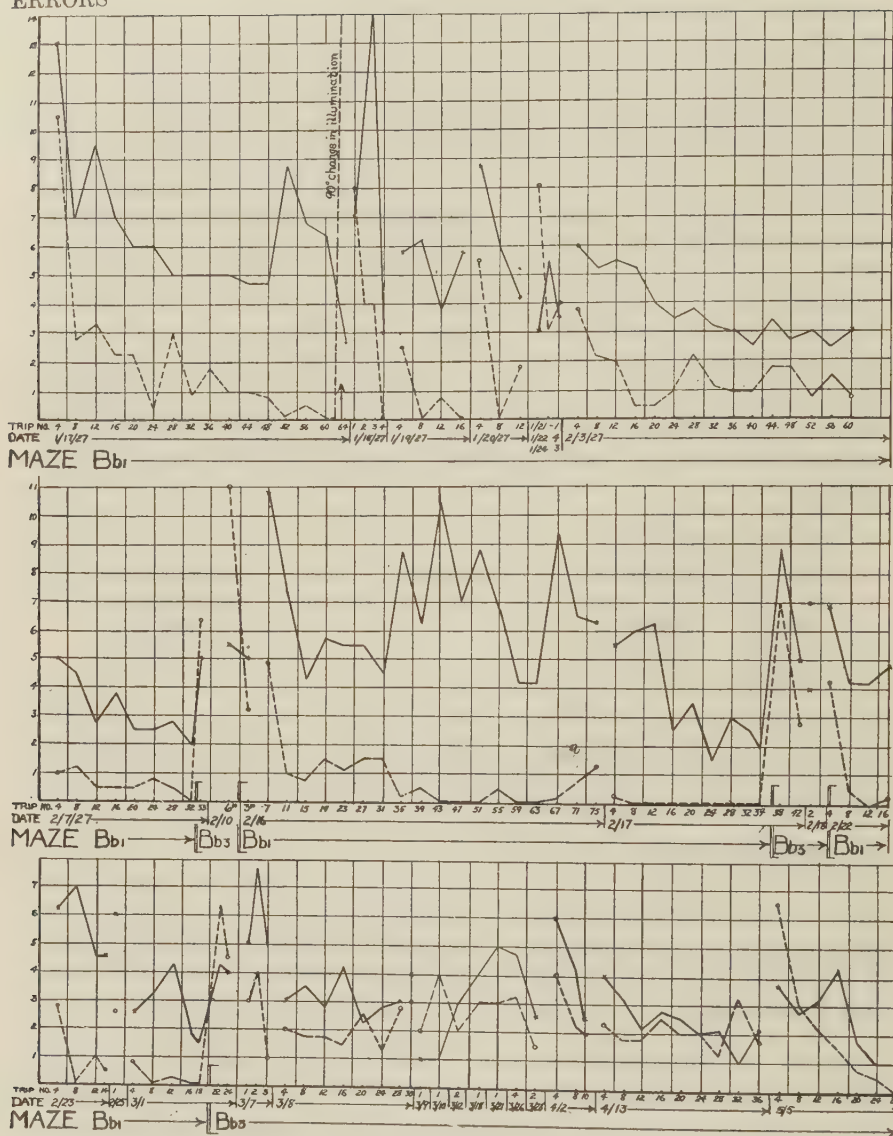


FIG. 7. SAMPLE MAZE RECORD OF INDIVIDUAL ANT (ANT 'z', *F. subsericea*), FROM JANUARY 17 TO MAY 5, 1917

Trips to food-box, ———; trips to nest, ----- (Illumination from the right side of maze, excepting trips 63-64, 'z', January 17.),

The general account of the behavior in the maze (Appendix I) should be examined in connection with the series of curves (fig. 7) showing the ant's progress in maze-running efficiency. Later in the paper we shall study the special features of this record in some detail (pp. 57-62, 86-93.)

c. Learning, when the food-place is varied in position. In our principal experiments on learning it was necessary for the ant to pass always to the same place (food-box) in order to obtain food to carry to the nest. Yet under natural conditions it is more often necessary for a forager to go on each trip to a somewhat different place for a burden. The writer has duplicated this condition in the maze situation. In the sample case discussed below, food (small particles on a piece of bristol board) was placed in a different alley corner of the maze and nearer the food-box for successive trips.

The ant labelled 'diamond,' *F. subsericea*, was a member of a group marked nine days before the experiment was performed, and had not been in maze *Bt1*, the pattern in which the tests were conducted. The customary procedure was effective, including the regular exchange of alley linings at the junctions. The following data was obtained for the first twelve trips:

TABLE 1
Sample of results for the variable food-place experiment
(Ant 'diamond,' *F. subsericea*)

TRIP NUMBER	ERRORS		FOOD FOUND IN	FURTHEST ALLEY REACHED
	Previous to finding food	After finding food		
1	9	13	5b	7b
2	10	21	5b	7d 1/5
3	5	16	6a (end)	7c
4	7	13	7b 1/2	7d (end)
5	4	10	7a (end)	7b 1/5
6	11	12	7b (corner)	7b
7	6	3	6a (end)	7b 1/3
8	5	3	Food-box	
9	7	0	7a (end)	7b 1/5
10	7	1	Food-box	
11	4	3	Food-box	
12	1	2	Food-box	

The results show an evident decrease in the errors committed, although on each trip it was necessary for the ant to pass through a greater portion of the maze in order to find food. If a curve is plotted to show the number of errors made before the food was found in each case, and another to show the errors made after the food was found and before the nest was reached, each of the curves shows an unmistakable decline as the number of trips increases. In addition, if one takes a constant point reached or passed on all of the trips (alley 5b), and makes comparisons as to the errors made previous to reaching this alley, or as to the errors made after passing the alley on the way to the nest, a decrease with further trips is found in both cases.

This condition is more often the case for food-finding in the open, where the forager must procure dead insects and other food that is scattered about in the vicinity of the nest. Since any one individual worker usually forages in a single direction for a considerable time, and makes many returns to the nest with food that is found, our experiment coincides with field observations in showing that learning progresses in spite of the fact that the ant acquires a burden in a different place on each trip. This indicates the complexity of the learning process involved in the normal food-foraging behavior. It is plainly necessary to consider the problem not only as a matter of learning to reach a certain place, and to return from it to the nest, but also to take into account the importance of the various local sensory-motor situations.

d. Elimination of the tendency to enter blind alleys. In the general problem of maze-learning, perhaps the most important feature is the manner in which the animal comes to avoid the detours from the main path that are involved in the entering of blind alleys. We have planned one of our mazes (Bb1) so as to make the regular entering of three blind alleys almost a certainty, and thus to permit a detailed study of the elimination of the 'coerced' behavior. On the other hand, by reversing the operation of the influence which enforces this behavior, it is possible to plan a pattern situation that almost completely prevents the entering of the related blind alley. From the first

trip, then, there may be important differences among blind alleys as to the tendency to enter them, and therefore as to the ease of their elimination. We shall review sample records which illustrate the important contrast between the first two types of the following classification.

Types of blind alley

Type 1. A blind alley whose primary entrance is 'favored'³⁰ from the start by 'centrifugal swing' (see p. 68 f.), and which is therefore eliminated only after considerable difficulty. Example: Blind alleys 4, 6, and 8 in maze Bb1, for trip to food-box.

Type 2. A blind alley whose primary entrance is 'opposed' from the start by centrifugal swing. Examples: Blind alley 4 in maze Btl, trip to food-box; and any one of blind alleys 8, 6, or 4 in Bbl, or blind alley 6 in Btl, for trip to nest.

Type 3. A complication of the above conditions, by changing former blind alley to true pathway, or the reverse, in altering the pattern of a maze after it is once learned (see pp. 79 ff.)

(1) *Elimination of blind alley Type I.* The situations encountered on the trip to food-box through pattern Bb1 proved so difficult that only five of the record ants progressed very far in eliminating the tendency to enter the three blind alleys (4, 6, and 8). The records for these ants are quite in agreement on essential points. For convenience we shall use as our example the records for an ant whose behavior is reported in some detail in Appendix I (and fig. 7), ant 'z,' *F. subsericea*.³¹ The treatment

³⁰ 'Primary entrance' to a blind alley (or true path alternative) occurs when the turn to this alternative follows directly the exit from the preceding true path alley. 'Secondary entrances,' returns to the blind alley from other parts of the maze, are uniformly eliminated early in the course of learning. A blind alley (or true path alternative) is 'favored' when centrifugal swing operates to bring about primary entrance to this alley rather than to its alternative.

³¹ Fig. 8A, presents a graphic record of the extent to which each of the three blind alleys (4, 6, and 8) was entered on the trip to food-box, during the first part of ant 'z's' record in maze Bb1. Against the TRIP NUMBER on the abscissa, the DISTANCE to which any one blind alley was entered is indicated by height above the respective base line on the ordinate. For each alley situation, entrances into the second arm (e.g., to 4a) are plotted as distances above the median line. Each end-for-end turning of the true path—blind alley lining at any one junction is indicated by an arrow pointing downward at the trip number for which the change

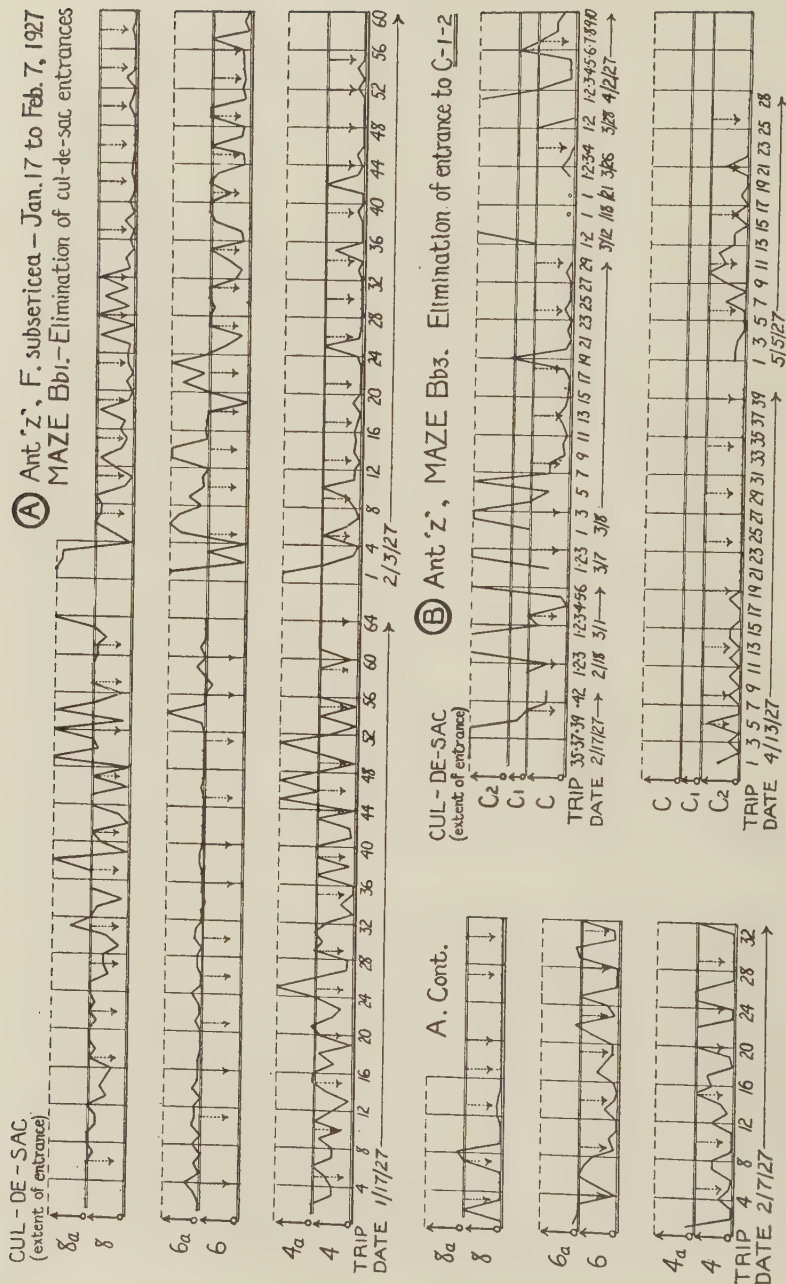


FIG. 8. A, ELIMINATION OF THREE "COERCED ERRORS" IN THE ORIGINAL PATTERN Bb1. B, ELIMINATION OF A FORMER "TRUE PATHWAY" HABIT, -MADE A CUL-DE-SAC IN Bb3

Note: Distance above base-line shows extent of entrance; arrows designate lining exchanges at junctions

will be based upon the detailed course by which cul-de-sac 8 was eliminated as an error.

Elimination of entrance to 8a (second arm of 8). Considering first the behavior in 8a, the second arm of alley 8, we find that beginning with the first trips, on Jan. 17, contact with the end of the first arm (8) was generally sufficient to bring a return toward alley 9. In fact, the second arm was not entered at all until the 31st trip, and then but half its length. On trip 38 the second arm was entered to its end, although it had not been passed into since trip 31, and subsequently it was not entered before trip 49. After that it was entered three more times, at sporadic intervals, and but once during the last ten trips.

On February 3, alley 8a was entered almost to its end on each of the first three trips, but was not entered on any of the remaining 57 trips for that day.

The February 7 trips included but one entrance into alley 8a, for a short distance (trip 8).

It should be said that in most cases, and especially for *F. exsectoides* individuals, there was a greater tendency to continue to enter alley 8a, a tendency which nevertheless eliminated itself relatively quickly, and in a manner somewhat similar to that in which the first arm was subsequently dropped. Ant 'z' was an unusually rapidly moving individual, who turned quickly on contact, while the more slowly moving ants were more likely to continue in contact with the wall encountered at the end of alley 8, thus passing into 8a.

Elimination of entrance to alley 8. For the first few trips on January 17 (original maze experience for this ant), 'z' usually entered alley 8 to its end, and upon contact with the wall would turn to pass into alley 9, with the possibility of making secondary entrances into 8 from one of the alleys of situation 9. However, the figure shows an early tendency to turn back to alley 9 before the end of alley 8 had been reached, and the distance through which 8 was entered before this turn was made was seen to decrease with further maze trips. The exchange in pathway linings at the junction interfered somewhat with this shortening tendency, since each of the first three changes in the linings caused alley 8 to be entered its full length. After each trip for which an exchange was

was introduced. This chart presents the course of elimination for the first 156 maze trips completed by 'z',—enough to show the complete elimination of alley 8, the relatively complete elimination of 4, and the partial elimination of alley 6 as errors.

made, there was an evident return of the shortening tendency. With further trips the interference decreased in effect. On trip 39 the figure shows the first direct (primary) entrance into 9 from alley 7b. On the following trips there were other direct entrances into alley 9, but this progress was interfered with, on trip 49 and those following, by excitement based upon a vibratory disturbance.³²

On February 3 the shortening tendency again appeared. Up to trip 33, the short and long entrances into alley 8 alternated. (In this connection we may note a fact that will become more evident later: *The entrances are either approximately full length or for a relatively short distance into a blind alley that is in process of elimination, rather than decreasing gradually in length. It is by the alternation of these conditions, the short entrances becoming more frequent with further trips, that the error is at last completely eliminated.*) After trip 34 alley 8 received no entrance for more than one-fourth its length; and mere hesitations at the junction, slight 'dips' into the alley before turning rapidly into 9, and direct entrances to alley 9 become increasingly frequent. (Total, 140 maze trips to date, including the trips on scattered occasions between 1/17/27 and 2/3/27.

February 7 On the resumption of maze passage four days later, the process of elimination reached its completion. Alley 8 was entered to its end, on the second trip, and again on the 7th and 8th trips. The latter entrances into 8 were due to the hesitant and slow progress through alley 7b caused by the substitution of a new alley lining in that alley. There was a slight recurrence of this behavior when the original lining was reintroduced on the 12th trip (see curve), but further exchanges produced no effect. (As an olfactory control, the end-for-end turning of the original 7b lining, before the exchanges were begun, was without result.) Primary entrance into alley 9 was the rule for the remaining twenty trips preceding the change to pattern *Bb3*.

Our discussion of the elimination of entrance into alley 8 holds in general for alleys 4 and 6, as well. In the case of ant 'z', alley 4 showed the tendency toward elimination earlier than did alley 6. During the first 64 trips in the maze, on January 17, primary entrances into alley 5 were more frequent as the number of trips increased, and there was a concomitant tendency to enter alley 4 for shorter distances. Alley, 6,

³² Throughout the study we shall find evidences of this fact: Any influence that increases emotional behavior will interfere with the course of learning, leading to a greater variability in maze behavior and to a greater susceptibility to the effects of such influences as centrifugal swing, 'minor chemical differences,' etc.

on the contrary, was entered first each time after exit from alley 5b, and consistently to its end, as figure 8 A shows. Nevertheless, there was an early tendency to abandon even a short entrance to the second arm, 6a, and this entrance was eliminated by means of a growing inclination to turn directly upon contact with the end of alley 6.

On February 3, the elimination of alley 4 continued, there being many primary entrances into alley 5,—in fact, during the last twelve trips there were but two short primary entrances into 4. The above italicized statement concerning the manner of dropping an error through the alternation of short and long entrances to the blind alley, is also evident in the case of alley 4, and of 6. As for alley 6, there were distinct indications of the elimination of primary entrance into it; there being an increasing proportion of short entrances, although primary entrances into 7 were few.

February 7 brought an increasing frequency of primary entrances into alley 7. The tendency to shorten entrance into alley 6 grew, most of the entrances now being for no more than one-sixth its length. . . . On February 16, the elimination of alley 6 continued further, as shown by the following data.

Situation 6-7 (Bb1). February 16 (74 maze trips)

Extent of entrance:

	<i>Number of entrances</i>
Primary entrances to alley 7.....	47
Primary entrances to the end of alley 6, a few to end of or part way into 6a.....	13
Primary entrances to 6, for no more than one-fifth its length.....	14

Although, on days when many maze trips were given, the progress of elimination continued further than the stage indicated above, the consistent primary entrance into alley 7 was not (in the course of 496 maze trips) completely established. There was always some vestige, however slight, of the tendency to enter alley 6. This fact is shown by the following tabular presentation of the results for the last trips of April 13 and the trips of May 5.

Situation 6-7 (Bb1). April 13 (last 19 trips)

Extent of entrance:

	<i>Number of entrances</i>
Primary entrances into alley 7.....	12
Primary entrances into 6 for no more than one-tenth its length..	4
Primary entrances into the end of 6.....	2
Primary entrances into the end of 62.....	1

May 5 (25 trips)

Extent of entrance:

Primary entrances into 7.....	15
Primary entrances into 6, for less than one-fifth its length.....	6
Primary entrances into the end of 6.....	3
Primary entrances into the end of 6a.....	1

(2) *Elimination of blind alley Type II.* Kinaesthetically considered, type 2 is the opposite of type 1. In the case of type 1, primary entrance into the blind alley was overwhelmingly favored, and a great number of maze trips was required to eliminate the tendency, whereas the true path alternative to the type 2 blind alley was favored in the same way. Consider the following results obtained for four ants in a blind alley of type 2.

*Typical results for situation 4-5**Maze Bt1, trip to food-box*

Ant '3', *F. subsericea* entered alley 4 one-fourth its length on her 12th trip, and hesitated at the junction on trips 4 and 8, for which lining exchanges had been made. On the remainder of the forty trips made during her original day in the maze, this ant passed directly and rapidly into alley 5 each time.

Ant '7', *F. subsericea* made two entrances into 4, —on her 3d trip, to 1/5 its length, and on her 5th trip, to 1/2 its length,—both of these due to preceding exchanges in linings at the junction. In each case the turn was made after some hesitation at the junction, the turn on the fifth trip being made after a sudden halt when the junction was reached. Further exchanges in linings had no influence on her consistently rapid turning into alley 5.

Ant 'O', *F. exsectoides* entered alley 4, to its end, on the eleventh trip, the climax of a rather slow, meandering journey through alley 3d. Usually, however, she 'hugged' the nest-ward wall of alley 3d, and turned directly and rapidly into alley 5.

Ant 'i', *F. exsectoides* made one or two hesitations at the junction on the occasion of the first exchanges in linings, but in all cases there was a direct turn into alley 5.

All cases were the same,—the true pathway turn had by far the greater advantage, and only as a result of the brief initial

disturbances caused by the exchange in pathway linings at the junction was alley 4 entered. With regard to its significance in the pattern, this type of blind alley occupies a position analogous to that of the true path alternative to the type 1 blind alley. Only as a result of long effective local conditioning (learning) was the type 1 blind finally eliminated as an error, but in the case of type 2 this conditioning influence operated only to increase the rapidity and smoothness of the movements made in turning into alley 5.

2. (*Learning*) *Summary and discussion of results.* From the foregoing results it is clear that the original learning of the maze is a true trial-and-error process, in the usual sense of the term. The general topic is not treated at any length in this paper, since Shepard's discussion, shortly to appear in print, will adequately treat the problem.

While the ant is becoming habituated to the maze situation, many irregular errors are committed, due to the random running about over walls and ceilings of alleys, and to other unpredictable behavior. These erratic movements disappear early in the course of learning, being mainly responsible for the relatively rapid initial drop in the curves. In addition, there is a tendency, as in other animals, to make random returns in open true path or in blind alleys, without having come to the end of the alley. This behavior, as well, is soon eliminated, although it persists longer than that discussed above.

There are more stable errors, many of them due to difficulty in making the 90° and 180° turns in true pathway. These mistakes may be partially due to failure to change the axial position of the body with respect to the principal direction of illumination, but they are more directly caused by a tendency to turn back upon contact with a surface (end of an alley). As the ant becomes habituated to the separate alley situations, there is a consistently increasing tendency (greater if the ant moves rapidly) to turn to one side or the other upon making such contact, and thus there is greater likelihood of a turn into the next unit of true pathway than of a complete reversal of direction. This type of error also drops relatively early in the course of learning, the inability to make a 180° turn persisting the longer.

In the writer's studies there were other errors incident to the exchanging of true-blind alley linings at the junctions. These errors were also effective for some time in the early course of original learning, although they were usually eliminated in the course of approximately fifteen maze trips.

To sum up, learning progresses in the elimination first of the irregular and random movements, and later in the elimination of the more stable errors in the course of a consistently growing sensory control of the most efficient responses.

Finally, there are errors whose original is inherent in the nature of the maze-pattern itself,—'imposed' upon the animal, as it were (type 1). The observations on behavior in blind alleys of types 1 and 2 offer a contrast that throws into relief the strong conditioning process that operates in favor of a direct entrance to the true pathway alternative, in any case. The tendency to enter the type 1 blind alley is strong, yet we have seen that even this influence is neutralized in time. The writer has studied the course of this elimination in some detail, and finds it possible to sketch its usual progress as follows:

(1) At first, the ant enters the blind alley to its end, and turns back upon contact with the wall.

(2) Then, alternating with condition 1), there are trips on which the return is made after the blind alley is entered only a short distance. The latter gradually predominates, and comes to alternate with

(3) a tendency to make a direct turn into the true path alternative, without entering the blind at all. This behavior gradually becomes more frequent, and may become completely established after a great many (two hundred or more) maze trips.

The elimination of these strongly enforced movements is an interesting process, and the fact that it does come about in time is of great importance. The first steps in the explanation of this elimination process must be based upon a thorough analysis of the changes that occur in the control of movements, as learning progresses. In the next section we shall find a number of facts that have much significance for such a study.

There is a further point which, although it is not to receive detailed treatment in the present paper, is of basic importance for these experiments,—the possible relationship that the runs through the maze in the two directions may have to each other. Especially important is the fact that the carrying of food from the food-box to the nest apparently operates to influence characteristically more regular and unemotional behavior than is the case for the unladen trip from nest to food-box (see Appendix II). In many cases an intense and continuous vibratory disturbance produced very uncoordinated behavior and sporadic errors during the trip to food-box, but failed to disturb the ant much while she was passing with food to the nest. For example, ant 'z', an individual that was relatively easily excited, showed rather consistently erratic behavior on her trips to the food-box during or following a disturbance, but the corresponding trips to the nest were usually quite rapid and efficient (see Fig. 7, curve for February 16, and Appendix I, notes for the same day). There are other results that agree with these to show that the trips in the two directions through the maze represent essentially separate and independent learned series of movements.

C. The kinaesthetic (proprioceptive) and contact factors

I. General remarks and historical resumé. It is a well-known fact that ants have a surprisingly powerful musculature. Their long striated muscles,—each stria composed of a great number of contractile elements, whose action enables the externally placed chitinous skeleton of the body segments and leg parts to be moved as powerful systems of levers—are developed quite out of proportion to the animal's size.

The motor innervation of these muscles is fairly well known in general, as is also the presence of centripetal fibres, but the more intimate relationship of these to the central system of ganglia—i.e., the extent of the course of neurones of the first order through the inter-segmental connectives, and their secondary relations with higher ganglia of the system—has yet to be worked out in significant detail.

We may reasonably infer that the muscles have a fairly rich sensory innervation. Also, few movements made by ants are strictly local in character; the entire body seems to participate in even the minor types of activity. Hence no movement can be made without arousing a configuration of contractions in leg,

thorax, and head muscles, giving a corresponding pattern of centripetal nervous impulses originating in the proprioceptive (kinaesthetic) endings of the muscles involved. A priori, it follows that each movement must be an important factor in determining the nature of the next.

Summing up, serial responses may be given to successive kinaesthetic configurations, in which each complex movement provides an essential portion of the stimulus situation which arouses the next one. It is apparent that muscular responses may be coördinated into series established on this basis. Thus, centripetal fibres from proprioceptive endings in muscle are very important, but they should not be considered apart from their possible relation to the fibres carrying impulses from the other receptors of head and body. No receptor-system can be isolated, and treated by itself in the matter of origination of responses and their subsequent coördination.

In this section it will be our object to show the importance and necessity of studying the movements that any situation imposes from the start, and the relation of these 'coerced movements' to the gradually established series of coördinated responses. This will bear out the importance of the point stressed above. We shall also undertake to suggest the close relationship that the proprioceptive possibilities of an orienting situation may have with the contact stimuli; to show how the former play an important rôle in setting off movements which bring the latter into function as local and more definite controls of finer adjusting movements.

It is as true for the ant as for any other animal with exteroceptors and proprioceptors and with muscles, that the study of its orientation should involve a thorough examination of the possible intimate relation that the proprioceptors and contact-receptors may bear to the control exerted by the head and body exteroceptors. Further, it is important to study the way in which the receptors may vary in this integrative coöperation, in initiating movements made at different stages of the learning. The first of these questions must be understood before the second can be treated comprehensively.

Previous attitudes as to the importance of the proprioceptors in ant orientation—

Piéron's phenomenon has been explained by assuming a "pedometric sense" and a "muscular memory," the former to account for the ant's ability to stop after an appropriate distance has been covered on the new parallel trail, the latter for the assumed ability of the animal to retrace its outgoing course in returning to the nest. After lateral transport, following the making of a certain series of movements and the expenditure of an appropriate amount of effort, it has been suggested that the pedometric sense functions to call out "searching movements" for the nest opening (see pp. 77-79).

Cornetz (p. 8f.), examining the muscular memory concept (1909-1914), endeavored to show by numerous traced paths of *Myrmecocystus* and other species that the ant on her homeward trail reverses only in a general manner the path taken on the outward course, in that the resultant direction is opposite, on the whole, to that of the outward trip. He found the ants to maintain a principal direction ("Constancy rule"), but in no sense did Cornetz believe the specific movements made on the outgoing course to be related to those of the homegoing. He denied the function of the muscle sense as described by Piéron.

Szymanski interpreted the results of his "Ablenkungsversuch" to prove the existence of a "sense of angles." As we have seen, Brun repeated this experiment for a number of species, but did not agree with Szymanski in the interpretation of the results. Rather, it was Brun's conclusion that the basis for the ant's ability to "close triangles and polygons" in proceeding to the nest after being released from the constrained course usually is a reference to large nearby objects (houses, trees, etc.). It is significant that the experiment failed for a poorly visioned species and for artificially blinded ants.

Although it is doubtful that a "Winkelsinnes" exists, there are many other ways in which the proprioceptors can be of importance in orientation. Turner (1907) found that after ants had learned a path down an incline leading in one direction, it was very difficult for them to take the path when the incline was tilted upward in the same direction. Similarly, Brun found ants

able to use angular deviations (from the horizontal) in their orientation. Not only are his results valuable in showing that such a differential kinaesthetic control of movements is possible, but also in demonstrating that its rôle varies according to the possibility of control by the exteroceptors (vision, in his experiment).

Another of Brun's experiments demonstrated that the direction of a 90° turn may be "engraphed" by ants. When passing to the nest from the center of a bridge involved a different series of movements from that required to pass toward the platform—as was the case when the two lateral detours led in the same direction from the main path—the ants seemed to have "engraphed this apparently complicated kinaesthetic succession." The writer's maze experiments show that this type of kinaesthetic control can be far more involved than was the case in mastering Brun's simple pathway.

Shepard found that the more rapidly moving ants were able to pass successfully through the maze alleys when the maze was darkened, whereas the slowly moving individuals appeared disoriented. It was concluded that the apparently greater independence of the light shown by the rapidly moving ants was based upon their ability to use a kinaesthetic control which the more slowly moving ants had been less successful in acquiring. Shepard believed this kinaesthetic control to be of considerable importance for the species investigated by him, though not as effective as the visual and chemical factors.

2. *Centrifugal swing: Coerced movements in maze-learning.* At present, it is not our purpose to attempt an exhaustive investigation of kinaesthetic control in orientation, but to lead to such a study by examining influences which have been found very effective in determining the nature and extent of the kinaesthetic function. The most important of these influences, as it operates in learning of the maze, is effective from the start.

An ant in the maze for the first time does not behave in a purely 'random' manner, running about erratically until she either blunders back to the starting point or through to the food-box. Rather, within limits the observer can accurately predict the behavior of the animal, provided the significance of certain

pattern features of the maze is known to him. The spatial arrangement of the maze alleys (or, under natural conditions, of tree trunks, stones, etc. about which the ant must detour) is important for the influence we shall term *centrifugal swing*, an influence to which the ant is very subject. In general, it depends upon the physical fact that in passing around a corner with reasonable speed, the animal must run near the outside walls³³ of the turns, until compensatory movements restore the normal center of equilibrium. While the ant is under the influence of this centrifugal swing, movements compatible with it (turning into a type 1 blind alley, for example) will be easily made.

Before considering the results obtained from the mazes specifically designed to test the effects of centrifugal swing, we shall briefly describe the way in which the experiments with maze *A* (fig. 3) first brought the matter to attention.

The notes for early studies with maze *A* term alley-series 4-5-7-7a-8 a *trap*, since it was observed that relatively few of the ants (*F. subsericea*) ran into alley 9, although many succeeded in getting as far as alley 8. At busy times a number of ants were to be seen running back and forth between the blind alleys 8 and 4, with only an occasional one passing into alley 9, or through alley 3c toward the nest. The following individual record is typical:

(1) Reaching the end of alley 3, the ant comes into close contact with the left wall³⁴ of alley 3a through her momentum.

(2) Thence she comes into close contact with the *L* (left) wall of alley 3c.

(3) When this contact is removed (junction of alleys 4 and 5), the ant swings into alley 5, since the closeness of the contact has inclined her body in that direction when passing through alley 3c.

(4) Momentum carries her to the *N* (nestward) wall of alley 5, which she follows in contact.

(5) Following this outside wall (see note 33) in contact, the ant turns

³³ The term 'outside wall' here and throughout our discussion refers to the wall toward which the ant is centrifugally 'thrown' by the resultant momentum of her movements in passing through a series (L- or U-shaped) of alleys.

³⁴ For convenience, the four directions with respect to the sides of the maze are designated as follows: *N* is the side of the maze facing the *nest*; *L* is the side to the *left* of the nest, and *R* the side to the *right* of the nest; and *F* is the side opposite the nest,—i.e., the *food-box* side. These symbols are used to designate quadrants of the maze, and other features, as walls of alleys, directions in alleys, or the direction of illumination. (See figs. 3, 4, and 5.)

into alley 5a when contact is made with the wall at the end of alley 5. The outside wall of alleys 5 and 7 is now followed in contact.

(6) At the end of alley 7, a turn is made into 7a, and the momentum again increases the closeness of the contact with which the outside wall of alley 7a is followed into alley 8.

(7) The ant is stopped by the 180° turn to alley 8b (or by the 180° turn to 8d). Turning around, she tends toward the *F* wall of 8, and follows this to alley 7a.

(8) She runs through alleys 7 and 5a in contact with the *L* wall, and thence follows the *N* wall of alley 5 into alley 4, where the behavior of situation 8 is duplicated.

If the ant continues to move rapidly, there is considerable probability that the above sequence will be repeated a number of times. The writer has seen ants wander in the above manner for more than an hour, without getting from the situation to alleys nearer the food-box or nearer the nest.

It will be observed that the key feature of this 'trap' is the fact that two turns in the same direction (i.e. into alley 5a from 5 and into 7a from 7, or vice versa) 'throw' the ant into close contact with the outside wall of the third alley. The following principles are fundamental:

a) *If the maze pattern includes two or more turns in the same direction (i.e., two or more successive turns to left or to right) as integral parts of a succession of alleys, when passing through these alleys the ant will be 'thrown' (by means of her momentum) into close contact with the outside wall of the second alley, and into more intense contact with the outside wall of the third alley.*

b) *Observations on turns made from alley 3c into alley 5, in maze A, (and similar situations), show that if an ant follows an alley wall (toward which she has been thrown by the centrifugal swing of a preceding turn) in close antennal contact, and if this alley opens into two alternative alleys running at right angles to it and leading in opposite directions (i.e., a T-situation), she will turn into that one of the two alleys which lies on the side of the previous close antennal contact.*

This description should not be taken to imply that the initial maze behavior is rigid and inflexible. Although the above two principles are of fundamental importance, there are exceptions which depend upon the speed of the ant, her tendency to make irregular returns in open true pathway and erratic movements, and other incidental influences.

a. *Operation of centrifugal swing in mazes Bt1 and Bb1.* As we have said, one of the important considerations in designing the patterns *Bb1* and *Bt1* was to enable testing the influence of centrifugal swing in relation to contact and other factors. In planning *Bb1*, three of the blind alleys were made Type I (see p. 57) for the trip to food-box, and Type II for the trip to nest (blinds 4, 6, and 8). For the trip to food-box through *Bt1*, alley 2 was 'impartial', alley 4 was Type II, and alley 6 was Type I; while for the trip to nest through this maze alleys 6 and 2 were Type II, and alley 4 was Type I.

The following description of the characteristic behavior in the several alley situations of the two mazes, when compared with the data in tables 2 and 3, shows the extent to which the planned pattern relationships introduced the influence of centrifugal swing in each case.

TABLES 2 AND 3

Tables presenting number of primary entrances to each of the blind alleys in mazes *Bt1* and *Bb1*, considering in groups of ten the first fifty trips made by three representative individuals for each maze

TABLE 2

Primary entrances to blinds of *Bt1*, per groups of ten trips

	TRIPS	TRIPS TO FOOD-BOX			TRIPS TO NEST		
		Alley 2	Alley 4	Alley 6	Alley 6	Alley 4	Alley 2
Ant 'O', <i>F. subsericea</i>	10	2	3	8		6	
	20			2	1	2	1
	30				2	1	
	40			3	1	1	
	50			1		4	
Ant '7', <i>F. subsericea</i>	10	3	2	3	1	6	1
	20	3		6		2	
	30	1		10	3	2	
	40	1		10	2	1	1
	50			1			
Ant '3', <i>F. subsericea</i>	10	3		8	1	5	1
	20		1	6	2	9	2
	30	2		9	1	7	1
	40	1		9	2	3	
	50			1		1	

TABLE 3
Primary entrances to blinds of Bb1, per groups of ten trips

	TRIPS	TRIPS TO FOOD-BOX				TRIPS TO NEST			
		Alley 2	Alley 4	Alley 6	Alley 8	Alley 8	Alley 6	Alley 4	Alley 2
Ant 'dot,' <i>F. exsectoides</i>	10	4	10	10	9		1		1
	20	3	9	10	8		1		
	30	1	10	10	9	1			
	40		8	9	9				
	50	1	7	10	7			1	
Ant 'd,' <i>F. subsericea</i>	10	3	6	6	7	2		1	1
	20	4	7	10	9	2	2	1	
	30		9	10	10			3	
	40		10	10	9	1		3	
	50		8	8	10	1		3	
Ant 'z,' <i>F. subsericea</i>	10	2	10	10	10	1	2		1
	20		10	10	10		3		
	30		10	10	10		1		
	40		8	10	9		2		
	50		9	10	7		1		

Behavior in alley situations of maze Bt1.

Maze Bt1, *trip to food-box* (see table 2).—

Alley situation 2-3: A rapid elimination of primary entrance (see note 30) into alley 2 was the rule, obviously due to the fact that centrifugal swing was not effective.

Alley situation 4-5: There was consistent primary entrance into alley 5 (see p. 62f.) from the start, although the exchanging of linings at the junction sometimes interfered to a slight extent on early trips.

Alley situation 6-7: There was a tendency toward primary entrance into alley 6, due to the fact that the opposition of the two preceding turns led to close contact with the *R*-wall of 5d, leading to contact with the *F*-wall of alley 5e and consequently to a turn into alley 6. Hence this alley was Type I, but indirectly through the operation of centrifugal swing. All of the ants succeeded in eliminating the turn into 6 in favor of a direct turn into alley 7.

Trip to nest—

Alley situation 7-6: Primary entrance into 5e was the rule, due to the enforced close contact with the *L*-wall of 7 throughout its length.

Some of the ants tended to overrun into alley 6 at times, when running too rapidly, or when excited.

Alley situation 5-4: Centrifugal swing imposed direct primary entrance into alley 4 on early trips, but this behavior was ultimately eliminated.

Alley situation 3-2: Primary entrance into alley 1 was the rule almost from the start. Centrifugal swing usually caused close contact with the *R*-wall of alley 3a—the main axis of the body maintaining an angle of nearly 90° toward the wall if the ant were moving rapidly—, and this contributed to a course in contact with the *N*-wall of alley 3, with a subsequent turn into alley 1. This is quite similar to the behavior reported for situation 6-7, trip to food-box.

Maze Bb1, *trip to food-box*—(see Table III)—

Alley situation 2-3: See situation 2-3 in Bt1 (trip to food-box).

Alley situations 4-5, 6-7, and 8-9: There was consistent primary entrance into the blind alley in each case, which was eliminated only with difficulty at an advanced stage in the learning (see pp. 57ff.).

Trip to nest—

Alley situations 9-8, and 7-6: See situation 7-6 in Bt1 (trip to nest).

Alley situation 5-4: In general, the results were the same as those for situations 9-8 and 7-6, except that at times some of the ants tended to over-run the entrance to alley 3c. The length of alley 5 accounts for this fact (see p. 75f.).

Alley situation 3-2: See situation 3-2 in Bt1 (trip to nest).

b. Summary and brief discussion. We have shown the importance of the centrifugal swing factor for the maze-running of ants, by planning mazes on the basis of its influence. Depending on the fact that two successive turns in the same direction (i.e., to right or to left) serve to throw the ant into close contact with the outside wall of the last alley of the series, making it easy to turn into the next alley if it leads to that side (see p. 70), a true path-blind alley junction was introduced so that one or the other alternative was favored.

In maze Bb1, for the trip to food-box, three of the blind alleys were favored. As a result these alleys were consistently entered after all other errors had been dropped (see table 3, and pp. 57ff.),

and were eliminated with great difficulty. On the other hand, for the trip to food-box through either maze, the situation 2-3 was an impartial one in this respect, and entrance into the blind alley alternative was at first equally possible with that of true pathway, but was quickly eliminated.

If one plots the path taken by an ant in passing through the typical 'trip to food-box in *Bb1*' (Type I) situation, it will be found the same as that taken in passing through situation 4-5 in maze *Bt1* (Type II), except that in the latter case the influence of centrifugal swing is disposed in favor of entrance into the true pathway alternative. Moreover, the fact that in the situations 4-5, 6-7, and 8-9 in maze *Bb1*, the entrance to the blind alley was favored in going to the food-box, whereas the entrance to the true pathway alternative was favored in passing to the nest, is dependent upon the same principle.

Thus 'centrifugal swing' is an important influence in initial maze behavior, and is very effective in determining the control of movements as learning progresses.³⁵ Of course, its effect varies with the speed of the ant, with individual differences in general behavior, and with incidental influences, but our tables and reports have shown that we may consider these things equal, and still find a surprising uniformity in the maze behavior of different ants.

3. *Contact, kinaesthesia, and centrifugal swing.* In the above discussion we have established the manner in which centrifugal swing induces contact with one or the other wall of an alley, according to the spatial arrangement of the preceding alleys, and thus determines the direction of the turn that is made at the end of the passage.

Upon closer examination of this phenomenon, it is found that when contact is forced in this way, the ant first runs with her head close to the wall and with her body nearly at right angles

³⁵ There are many proofs that the important consideration in maze design is not the number of blind alleys in the pattern, but their spatial relationship with parts of the true pathway. For example, in later experiments the writer used pattern C1-2, which involved twelve blind alleys. Only two of the blind alleys were favored by centrifugal swing, and as a result the maze proved far less difficult than other patterns with fewer blind alleys.

to it, the antenna pressing so that it is almost doubled upon itself. Then, after a part of the alley is passed, the contact decreases in intensity and the body becomes nearly parallel with the wall. When the momentum of the ant's previous course toward the wall has passed, and contact is no longer enforced, can we predict the animal's next movements?

Alley 5 in maze *Bt1* was made rather long (three times the length of alleys 3, 7, or 9) in order to permit study of the above question. Whereas in passing through alleys 9 or 7, on the trip to the nest, the momentum accumulated from the two preceding turns would not have subsided before occasion arose to make the turn into the next alley, in this longer alley the last stage described above (decrease in the intensity of contact, parallel course with the wall) was usually reached after the ant had run through about one-third of the passage. This, of course, depended upon the running speed. Yet in practically all cases—from the first trip, as table 3 shows—, there was a direct turn from alley 5 into alley 3c. The maintenance throughout the alley of the originally enforced contact with the appropriate (*N*) wall of alley 5 was responsible for this. To account for the fact that the contact was sustained after the centrifugal effect had passed, we have only to recall that it is the almost universal tendency of ants, and in particular the *Formica* species, when in unhabituated situations, to maintain a contact until circumstances interfere with it. The tactual stimulus which led to the opportune turn was therefore a secondary or indirect effect of the centrifugal swing.

There is an interesting change in behavior as learning progresses. With further trips, in the case of alley 5, the ant passing toward the nest does not remain in contact with the favored *N*-wall throughout the alley. Instead, after the immediate influence of the centrifugal swing has spent itself, the ant takes a course nearer the middle of the alley, and occasionally comes into contact with the *N*-wall. Just before the junction with alley 3c is reached, however, she passes to the *N*-wall, makes contact with it, and turns when cessation of the contact provides the stimulus. In this process of finer tactile control, the development of a kinaesthetic regulation of the movements made in

passing through the alley plays no small part, as we shall show in analyzing its function (see pp. 77-79). Hence centrifugal swing and the tactual stimuli it affords are intimately related from the first stage of maze experience, and provide the basis for the integrated contact-kinaesthetic control that later develops. Having shown the importance of contact in controlling movements that are favored by centrifugal swing, our next step is to find what occurs in the opposite case.

When contact with the alley wall that is favored by centrifugal swing leads into a blind alley, a set of counter movements develops in the course of learning, off-setting the effect of the momentum from the preceding turns, and the contact is gradually shifted to the wall which must be followed if the direct turn into true pathway is to be made. In this transition the coöperation of kinaesthetic and contact control is outstanding, operating counter to centrifugal swing, although developing indirectly through its influence.

This learning is typified by the substitution of a direct turn from alley 5 to 3c (*trip to nest*, maze *Bt1*) for the tendency to pass along alley 5 into alley 4. The following illustration sketches in general this type of transition in movement-control.

In learning the passage to the nest through maze A, ant 'j' (*F. subsericea*) first displayed a strong tendency toward primary entrance to alley 14, passing to its end or further, into alley 14b. This consistent error was due to the effect of the preceding turns, which mustered a centrifugal swing that tended to throw the ant toward the wall of alley succession 17-15-14 opposite the entrance to alley 13, the next true pathway unit. Soon, however, there appeared a number of trips on which the alley 14 was not entered to its end. Finally, alley 13 was entered directly from 15, the tendency to enter alley 14 having disappeared. Nevertheless, the ant now began to enter alley 16. How is this to be explained?

During the early maze trips (a), the ant followed the outside wall of alleys 17 and 15, thus passing into alley 14, as we have described. On returning from alley 14, contact with the wall near 13 would permit an entrance to that alley. Sometimes, however, she did not hug this *L* wall of 14 in passing back, but followed the middle or opposite side of the alley into 15 or 17, where she turned and hugged the *L*-wall in

passing back to enter 13. This second stage, 'b,' really followed 'a' in the course of learning, although for a time the two possibilities were seen to alternate. Gradually, tendency 'a' appeared to decline, and 'b' was modified by a tendency to turn toward the *L*-wall of 17 after coming into this alley from 17a (c), and to follow this wall in a series of successive contacts. In time, the extent of this contact became less, and finally the ant was able to turn into alley 13 after but a short contact with the preceding small portion of the *L* wall of alley 15. It will be seen that the contact with the *L*-wall of the alley-succession 17-15, incident to steps 'b' and 'c', was the basis for the tendency to enter alley 16 that appeared later in the learning.

The above, of course, is not a complete description of the change in path that occurred as learning progressed. Between steps 'a' and 'b,' for example, there was usually a tendency to shorten the looping course of entrance to alley 14 and passage back into 17, and in most cases this was an essential step in the development of the tendency to turn directly to the *L*-wall of alley 17 after leaving 17a.

The above example shows the manner in which learning changes maze behavior by counteracting the influence of centrifugal swing. In other cases, where the fundamental behavior imposed from the start by centrifugal swing is fairly efficient (i.e., does not lead into a blind alley; involves no detours in true pathway), the conditioning effect of further maze trips acts to impress and further coördinate the movements. In this event, the kinaesthetic and contact stimuli that come to control the finally coördinated maze behavior are in large part the integrated sum of the stimuli originally afforded by the enforced movements themselves.

4. *The integration of contact and kinaesthetic control.* It is well known that an ant passing to the nest along an established path pauses as the nest is approached, and wanders about ("tournoielements de Turner") until the opening is found. According to Brun, the rapid course taken in reaching the nest depends upon a virtual orientation to certain general orienting factors—direction of the solar rays, etc. Cornetz (p. 8) and Brun (1914) have explained the pausing as due to the influence of various stimuli furnished by the nest vicinity.

The results of the Piéron lateral transport experiment (p. 7f.)

are related to this normal behavior. After being taken from the established trail, the ability of the ant to stop when she does on the new parallel trail has been accounted for by a postulated "fatigue sense," or on the basis of a "muscular memory" which operates to produce a halt after a certain number of movements has been made ('pedometer phenomenon'). Brun thinks that the general orienting features are effective in producing the rapidly travelled parallel course, but that when a "certain amount of effort" has been expended, the ant pauses. In addition, the absence of the "expected nest indications" seems to bring the pausing and the resultant searching movements sooner than would have been the case on the established trail.

Let us consider this behavior in the light of the conditioning process that probably is involved. During original learning, after a number of trips over a gradually straightening trail, certain stimuli incident to the vicinity of the nest (tactile, olfactory, and possibly visual) cause hesitating exploratory movements to follow the more rapid progress toward the nest. Thus the proprioceptive consequences of the last rapid movements, which otherwise would tend to produce further movements of the same kind, appear often enough concomitantly with the stimuli furnished by the nest vicinity to finally take over the function of the latter in bringing about the pausing and exploratory behavior. This is shown by the fact that the exploratory movements follow the rapid movements on the parallel course, when the Piéron transport experiment is performed. From this it appears that *in the ant the kinaesthetic stimuli furnished by a series of movements (or a movement) acquire, through a gradual conditioning process, the ability to call out further movements of a different kind.*

On this basis we may explain the maze behavior described above (p. 75f.). After many maze trips have been made, the ant is able to pass rapidly through the greater part of the alley,³⁶ and follows the 'near' wall in contact for a short distance preceding

³⁶ These rapid movements seem to depend upon the development of a virtual orientation to the direction of illumination.

the turn into the next alley. Relying upon the principle already established, it is not difficult to see that the kinaesthetic consequences of the last rapid movements are probably the effective stimuli for the arousal of the movements which bring contact with the wall. With respect to the origin of the coördination, this case is similar to that discussed above.

D. Relearning a maze following a local change in pattern

1. *The problem of the tenacity of maze habits.* The present discussion is properly a part of section 'B,' since it is essentially a study of the animal's ability to adapt to a changed situation. However, an adequate understanding of the situation actually presented to an ant forced to pass through an altered maze presumes to a considerable extent the material given in section 'C.' One must know the basis for degrees of difficulty in the original learning of various types of pattern before the significance of an alteration in the learned pattern can be adequately understood.

The most important feature of our experiments involving changes in previously learned maze patterns is the alteration of the true path—blind alley relationship at one or more junctions. In order to master a changed situation, a new set of movements must be established to take the place of the responses based on the original pattern conditions. Thus it is necessary to study the difficulty with which a tendency to enter the blind alley alternative was eliminated in the course of original learning, in order to compare this with the re-establishment of the movements when the blind alley becomes a true pathway turn. Again, it is desirable to compare the establishment of a true pathway turn in the original pattern with the rate of its elimination when the alternative is made a blind alley. In short, changed pattern experiments throw into relief the functions of the receptors in maze learning, and in particular they permit a further examination of the relation between centrifugal swing and contact-kinaesthetic control of movements.

Experiments were conducted for mazes *A*, *Bt1*, and *Bb1*, with

two local changes in pattern for each maze.³⁷ In our report, the results obtained from experiments involving one pattern change for each of the latter two mazes (*Bt1* changed to *Bt2*; *Bb1* changed to *Bb3*) will be treated in detail. Ant '7,' *F. subsericea*, (patterns *Bt1* and *Bt2*) is to be reported as representative of those ants which learned the pattern change on the day of its introduction, while the case of ant 'z,' *F. subsericea*, will exemplify pattern relearning that extended over a longer period of time.

2. *Illustrative examples of change-in-pattern experiments.* a. *Mastery of the change on the day of its introduction.* We have already reported the main features of the original learning of maze *Bt1* by ant '7,' *F. subsericea* (Section B). In forty-eight trips (March 3, 1927) this individual succeeded in learning the maze. Upon the completion of the forty-eighth trip, the change in pattern was quickly made while '7' was in the nest. The following is a condensed record of her behavior after the change was introduced.

³⁷ *Experimental conditions.*—Learning of the original maze pattern was required on the day of the change in pattern. (Due to the regular presence of the three coerced errors (p. 57) on the trip to food-box through maze *Bb1*, the required standard for that maze was five successive trips without errors other than the entrance into blind alleys 4, 6, and 8.)

As controls, three different portions of the maze (with respect to proximity to the food-box) were used to install the change in pattern. In *Bb1* the change was introduced close to the nest in making *Bb2*, and close to the food-box in making pattern *Bb3*, whereas in the case of *Bt1* the *Bt2* pattern was made by introducing the change at about the center of the maze.

Before the change was introduced in any case, a sufficient number of alley linings was saturated to provide units for the newly introduced alleys. This was done by regularly exchanging these pieces with linings in use on the original pathway, and in every case the exchange was performed for an alley in the region of the prospective change in pattern. No lining was used in a changed pattern until its regular exchange with a lining of the original pathway had ceased to produce an effect. (Early experiments failed because this fact was not adequately taken into account.)

Following three consecutive 'correct' trips through the original maze pattern, the change in pattern was introduced as quickly as possible, while the ant was in the nest after carrying food from the maze. In all cases, the direction of illumination was the same as in the original learning. The routine exchange of alley linings at the junctions was continued, this procedure being carried out for the newly introduced junctions, as well.

(1) *Record of the behavior (ant 'γ,' F. subsericea) following the change from pattern Bt1 to pattern Bt2 (fig. 4, 4a) . . .*

*Behavior, and errors made*³⁸

Trip number

44-48 Rapidly made, and without error for trips in both directions.

Change to pattern Bt2

49

To food-box—B1; B1; stopped in corner of B; B1; B1; A1/2; B1; B; B1; 3d; B1; A1; C1; A1. After getting into alley D (5e) she passed correctly through to the food-box, *her speed increasing greatly once the turn into γ had been made.*

To nest—C1; C1; stopped at the junction of A2-C. A2. Meandered somewhat in her progress through alley A, coming into contact with the *L*-wall of that alley just before turning into 3d. *She hastened as soon as 3d was passed.*

50 (linings exchanged at junction A-B)

To food-box—B1; B1; B; B; B1; (stopped in corner of B1); B1, crawled about near end of alley; B1; A1; stopped at junction A2-C; straight into alley γ from D, and very rapidly through the rest of the maze.

To nest—Retraced C 1/2 at its end; 7a 1/5; C1; 7a; 7 2/3; 7a 1/2; rapidly back to the changed part; C1; crawled to top of the bristol board obstruction at the end of this alley (formerly 5b): Now she passed directly from C into A2, and around the 180° turn into A with little difficulty.

51 (linings exchanged at junction 2-3)

To food-box—B1; retraced B 2/3 at its end; 3d; hesitated and turned at the corner between 3c and 3d; 3d 1/10; B; A1; now passed more rapidly around the corner into A2, thence directly into alley D and through.

To nest—C1 1/8 (barely put her head into C1 before turning back to C); relatively rapid course nearer the *L*-

³⁸ *Method of recording behavior in maze alleys:* Sample record, trip to food-box through pattern Bt2:

"3d; B1; A3; B1/2."—Retraced alley 3d, then passed to the end of alley B1, leaving this alley to pass along the true pathway. Turned back after passing through A3, and retraced the true pathway, passing half-way into alley B. Then turned to pass correctly through true pathway to the food-box.

Trip number

- wall of C-A2; through A1 and A correctly, hugging the *L*-wall of A for the half its length preceding the turn into alley 3d. Rapidly passed through the rest of the maze.
- 52 (linings exchanged at Junction C-D)
To food-box—B1; turned quickly to run through A and its sub-units; a little hesitancy on entering D from A2 (plainly due to the previous exchange in linings), but no returns. She veered close to the *N*-wall of alley D when nearing its end, and thus turned directly into alley 7.
To nest—C; hesitated somewhat at A2, but passed correctly and rapidly through. Hastened after A1 was reached.
- 53 (linings exchanged at junction 6-7)
To food-box—B1 9/10; slightly hesitated upon entering alley 7 from D, but there was no hesitancy in her course from A2 into D. From the past three trips the turn into D from A2 had been made more efficiently and rapidly each time.
To nest—C1 1/10. Rapidly through.
- 54 (linings exchanged at junction A-B)
To food-box—B1 1/6; A 3/4 (a direct effect of the lining exchange); B 1/2, then turned at once, and made a direct passage to A1 along the *R*-wall of B-A, with a rapid passage through the rest of the maze.
To nest—C 1/2; hesitated somewhat in A upon turning from A1 onto the end of the exchanged lining, but her course was not different from the usual one. (Note the way in which the entrance into alley C is being eliminated.)
- 55 (linings exchanged at junction 2-3)
To food-box—B1 1/8; A 1/6 (a slight hesitancy on coming to the end of the exchanged lining). The 180° turn from A to A2 was now being made by means of a direct cut around the inside corner, instead of following the outside, as before.
To nest—C 1/10.
- 56 (linings exchanged at junction A2-C)
To food-box—B; straight into alley D, without hesitancy or change in speed.
To nest—C 1/10 (merely a hesitation).
- 57 (linings exchanged at junction 6-7)
To food-box—B; A; B1 1/10.
To nest—No errors.

Trip number

- 58 (linings exchanged at junction A-B)
To food-box—B1 $1/3$. No hesitancy in passing through alley A, her course being near the *R*- wall of B-A. She passed through A1 close to the inside wall, making a sharp turn around this into A2, where she promptly veered to make contact with the *L*-wall for the turn into alley D. This was now the usual behavior.
- To nest*—Straight into alley A2. A slight hesitancy on coming to the end of the exchanged lining near the end of alley A, but otherwise a rapid passage.
- 59 (linings exchanged at junction 2-3)
To food-box—B. *To nest*—Rapidly through
- 60 (linings exchanged at junction 6-7)
To food-box—B. *To nest*—Rapidly through
- 61 (linings exchanged at junction A2-C)
To food-box—B 1 $1/20$. *To nest*—D.
- 62 (no lining exchanges)
To food-box—B, rapidly. *To nest*—Rapidly through
- 63 (linings exchanged at junction A-B)
To food-box—B1 $1/10$. *To nest*—Rapidly through
- 64 (linings exchanged at junction 2-3)
To food-box—B1 $1/10$. *To nest*—Rapidly through
- 65 (linings exchanged at junction 6-7)
To food-box—B. . . . *To nest*—Rapidly through
- 66 (linings exchanged at junction A2-C)
To food-box—B. . . . *To nest*—Rapidly through
- 67 (linings exchanged at junction 2-3)
To food-box—B $9/10$. *To nest*—Rapidly through
- 68 (linings exchanged at junction A-B)
To food-box—B. . . . *To nest*—Rapidly through
- 69 (linings exchanged at junction 6-7)
To food-box—B1. Hesitated at end of B, then rapidly to end of B1. *To nest*—Rapidly through
- 70 (linings exchanged at junction A-B)
To food-box—B. . . . *To nest*—A 2 $1/2$ to C $1/5$.
 First hesitated at the end of the exchanged lining in A2, and turned rapidly into C, but returned promptly after entering C but a short distance. All movements were very rapidly made.

Trip number

- 71' (linings exchanged at junction 2-3)
 To food-box—B. *To nest*—Rapidly through
- 72 (linings exchanged at junction A-B)
 To food-box—B 1/2. *To nest*—Rapidly through
- 73 (linings exchanged at junction A2-C)
 To food-box—B 1/2. *To nest*—Rapidly through

(2) *Curves for the relearning of a maze with changed pattern* The error and time curves for this learning are essentially alike. Consulting the error curves, which are more reliable, we find the following outstanding features:

a) The curves for error-commission begin at a lower point than do those for original learning. The evident basis for this fact is that the disturbance produced by the alteration of pattern is a relatively local one (see below), other parts of the maze being passed through much the same as before the change.

b) The curves for relearning of the changed maze are much more regular throughout their course than are the curves for original learning. (After a change in pattern, although disoriented in a portion of the maze, the ant does not behave as she did during the early part of original learning—running excitedly and irregularly about on floor, walls and ceiling of the alleys, etc.—, but now continues in her path until stopped by some feature of the altered pattern.) The persistence of the formerly effective responses leads, on the whole, to similar results in error-commission for each trip.

c) In all of the curves for the learning of Bt2 the course of the curve for the *trip to the food-box* is uniformly higher than that of the *trip to nest* curve, the two being approximately parallel throughout. This is due to the fact that the change in pattern introduced a 'coerced error' (B, formerly 5). In respect to this difference, and to the parallel course, the curves are similar to the original learning curves for maze Bb1.

d) These curves are not to be taken as representative of all relearning of changed portions of originally well-learned mazes. By appropriately planning the newly introduced alleys, it is possible to construct a changed pattern (e.g., a pattern in which persistence of the original maze responses will force repeated returns into the earlier part of the maze) that will lead to a far greater error-commission than was effective for the original learning. In this respect, there can be no general law for the relearning of mazes after the pattern is changed. Studies with maze Bb1-3 will further emphasize this point.

(3) *Localization of the disorientation produced by a change in maze pattern.* From the records it is clear that the immediate disorientation produced by the change in pattern was confined to the altered portion itself,—i.e., those alleys between 3d and the junction of 6 and 7. There was some likelihood that the persistence of the originally learned responses would lead to returns from the changed region to unchanged parts of the maze, and thus to temporary disorientation in the latter.

For example, on trip 49, immediately after the change, ant '7' retraced her path, from alley B to 3d, but quickly returned to the changed portion, in passing to the food-box; and on the trip to nest (trip 50) returned from alley C1 to 7, but after a very short period of wandering returned through alley D. In the case of '7', these were the only returns from the changed part to other alleys of the maze.

As a matter of fact, whenever any of the ants did make such returns, there was not much probability that the wandering would last long. Rather, the reorientation and the return to the changed portion of the maze was usually fairly prompt. Hence, for progress in either direction through the changed maze, the new series of movements may be said to have built itself from both ends of the changed part, with the unchanged responses made to the adjacent unchanged alleys as a basis.

A specific study of the behavior in certain of the new and altered alley situations will give an opportunity to see the nature of the adaptation, and will permit an answer to the questions framed on page 72.

(4) *General description of behavior in the individual situations.*

Trip to food-box (pattern Bt2):

Alley situation A-B (4-5 in Bt1). At the time of the change in pattern, passage from alley 3d to 5 had become a thoroughly established performance. In view of the ease with which this turn was made from the start (see p. 62f.), it is not surprising that the behavior persisted in the new situation, although the movements now led into a blind alley. In all cases the second arm of the blind alley was not entered after a few trips, but although all of the records show a tendency

to shorten the entrance into the first arm, none of the ants completely learned to avoid turning into the alley (within one hundred maze trips after the change in pattern).

Alley situation A2-C (new). Our previous treatment (pp. 68ff.) makes it unnecessary to dwell upon the fact that this situation offered few difficulties to any of the ants.

Trip to nest (pattern Bt2):

Alley situation C-A2 (90° true path turn in Bt1) During the learning of the original pattern, although the turn from 5e to 5d came to be made consistently without returns or other irregular movements, it was by no means 'favored' in the manner characteristic of the turn to alley 5 on the trip to food-box. A number of influences (opposing kinaesthetic tendencies due to the preceding turns in opposite directions, resulting contact effects, secondary conditioned hesitation related to the disturbance caused by the saturation of a new lining by exchanging it with the one in 5d, etc.) had been operative in producing variability in the manner of making this turn. As a result, the turning might come upon cessation of contact with the inside wall, as the result of following the outside wall and turning upon contact with the end, or as a result of crossing from one side to the other just before the turn. After the change in pattern, the tendency to make the turn to alley C (5d in Bt1) quickly decreased and disappeared, only seven trips being required in the case of ant '7,' and no more than ten in any case.

Alley situation B-A (new). See situation A2-C, trip to food-box.

b. Pattern relearning requiring a longer period of time (original and new conditions alternating). The preceding report shows the general characteristics of changed-pattern behavior. In contrast, the present treatment concerns a case in which complete mastery of the pattern change occurred only in the process of several re-introductions, and over a longer time. In experiments of this type, involving an alternation of the original and the changed maze patterns, there is an opportunity to study the conflict between different sensory-motor tendencies in the same situation.

It is expedient to choose a record that has already been presented in some detail (ant 'z' *F. subsericea*). The following is a condensed account of the behavior of this ant in the two main

alley situations involved in the alternate introduction of pattern Bb1 and its change Bb3. The reader may refer to Appendix I and figure 7, and to pp. 56ff.

(1) *Re-establishment in the changed pattern of an 'error' strongly favored and eliminated with difficulty in the original maze pattern.* During the original learning of pattern Bb1, entrance into *blind alley* 8 was favored by centrifugal swing, became a consistent error (trip to food-box), and was eliminated only in the course of a considerable number of maze trips (pp. 56ff.). The change to pattern Bb3 made alley 9 a blind alley, 'B,' and alley 8 became 'A,' the next unit of true pathway. During the last twenty trips on February 7 there was consistent direct entrance to alley 9 from 7b, the standard set for the change to pattern Bb3.

a) *First change to pattern Bb3 (2/7/27).* Although the first introduction of this pattern remained for only a few maze trips, there was a distinct tendency toward the elimination of primary entrance into the former true path turn (to alley B) and toward the re-institution of direct entrance into alley A (8 in Bb1).

b) *Return to pattern Bb1 (2/16/27).* When maze pattern Bb1 was replaced, again making A (8) the turn into blind alley, in all cases the tendency to enter this alley directly from 7b continued unreduced for a considerable time. This was quite in contrast to the relative ease with which the direct turn into alley 9 was eliminated when the change to pattern Bb3 made it lead into blind alley. It is true that for ant 'z' a vibratory disturbance heightened emotional behavior so that in the course of seventy-five maze trips on February 16 the primary entrance into this alley was not completely eliminated, but in the case of all other ants the 'renewed error' was dropped in from thirty to forty maze trips. (The secondary elimination was thus characteristically a much shorter process than the original elimination, and in most cases followed the typical course described for error-dropping during original learning (p. 60).) In the case of ant 'z', it is interesting to note that on February 17, when she had returned to the stability of unexcited maze-running, there were no direct entrances to alley 8 in the 16 trips preceding the next change to pattern Bb3. Only 18 trips were required for this to occur.

c) *Second change to pattern Bb3 (trip 35, 2/17/27).* For 'z', as for

other ants, the (restored) habit of turning directly into alley 9 (B in Bb3) broke down more easily than was the case following the first change in pattern that made it lead into a blind alley.

d) *Second return to pattern Bbl* (2/22/27). There was still less difficulty in eliminating the direct turn to A (8) than there had been for the previous change. An interesting fact is that on the first trips for February 23 and for March 1 there was a reappearance of the tendency to turn directly into alley 8 from 7b, but in each case it was short-lived, especially for the latter day.

e) *Third change to pattern Bb3* (trip 19, 3/1/27). After this change, it required only 7 trips, in the case of z, to bring a direct entrance to alley A (8). In all cases the consistent direct turn into this alley was re-established with greater ease than before.

Briefly, the above results show that it is relatively easy to break down a habit originally established with considerable difficulty in opposition to the strong influence of centrifugal swing (entrance into alley 9, maze Bb1). When a return to the original maze pattern again makes this turn lead into true pathway, the habit is restored with greater facility than was the case for its first establishment.

On the contrary, the greater the difficulty with which the tendency to make a movement was eliminated during original maze learning (i.e., the more powerful the influences in its favor), the more easily is the movement reinstituted when a shift in conditions makes this opportune.

Finally, the oftener the shifting of maze pattern changes the relationship of the true path and blind alley alternatives at a junction, the less is the difficulty with which adjustment is made to the change. The alternative favored by centrifugal swing is regularly re-established with greater ease than is the alternative that operates against this influence, but the true path turn eventually is the established one, in any case.

(2) *Successive substitution of a true pathway turn (original pattern) for an alternative (changed pattern)*. This condition is represented by the 90° turn from alley 9g to 9f (trip to nest, maze Bb1), which became situation A4-C when pattern Bb3 replaced Bb1 (Fig. 4). Obviously, in the learning of maze Bb1

the turn from alley 9g into 9f had been quite 'impartial' as to the influence of centrifugal swing. The following results offer an interesting contrast to those for situations such as B-A in maze Bt2 and B-A in Bb3 (trip to food-box).

After 'z' had learned pattern Bb1, the following experiments were performed.³⁹

a) *First change to pattern Bb3* (trip 33, 2/7/27).

February 7 From food-box to: C2; C1; C2 1/2; C2; A2; A1 1/2; to nest.

February 10

(1) From food-box to: junction A4-C, hesitating there; C 1/6; A3 1/2, retraced at end; D 1/2; C2 1/2; A3 2/3, retraced at end; thence returned to food-box. . . .

to: C2; A2; A3 1/2, retraced at end; C2, A2; C2; C1; C2 1/4; A2; C2 1/6, retraced at end; C2; A3 1/4; D 1/6; C2; A2; thence returned to food-box. . . .

to: junction A4-C, hesitating there, then passed toward the nest, hesitating again at A2.

(2) From food-box to: C2; C 1/2, retraced at end; D 1/2; C2; C1; A3 1/2, retraced at end; D 1/10; C1; to food-box. . . .

to: C 5/6; A2; D 1/4; C1; A4 1/2; A2; C; to food-box. . . .

to: C 1/2; A2; A3 5/6; to nest.

Of seven exits from the food-box, five primary turns were made into alley C. Following the primary turn, a direct persistence of the pattern Bb1 behavior, there was much disturbance when the end of alley C2 was encountered, and then wandering was the rule. After some time the ant would pass through situation A, turn directly into alley 7b from alley A (see situation 6-7, *trip to food-box* through maze Bt1, and Table 2, p. 71), and thence pass rapidly and correctly through the remaining alleys of the maze. The early appearance of hesitation at junction A4-C on

³⁹ Figure 8, B, shows the extent to which the alleys of situation C1-2 were entered on the trips from food-box to nest, following the successive changes to pattern Bb3. The relative distance to which the two arms of this situation were entered on the successive trips is plotted on the ordinate, against 'date' and 'trip number' on the abscissa.

coming from the food-box was probably an effect of the light that now reached this place through the A4 alley.

b) *Return to pattern Bb1 (2/16/27)*. After three incomplete trips on February 16, a change to the Bb1 pattern (alley C becoming true pathway turn 9f, the A4 alternative being eliminated) brought the following results.

February 16

- (4) From food-box to: 9f; 9d; 9g; 9f. Hesitatingly passed through the remainder of situation 9, and then rapidly went through the rest of the maze.
- (5) 'z' did not reach the food-box on the entrance trip.
- (6) From food-box to: 9f 1/2, retraced at end; 9f 1/2; 9c; to nest.
- (7) 9f 1/6; 9f; hesitatingly passed through to alley 9, then ran rapidly through to the nest
- (8) 9f 1/10; hesitated at 9c, then ran rapidly through the rest of the maze.
- (9) 9e 1/2; 9f 1/2; to nest.
- (10) 9e, hesitated; otherwise made a correct passage to the nest.
- (11) Retraced from 9f to 9g 1/2, then ran rapidly through the maze.
- (12) Passed correctly through, with a little hesitation at 9c.
- (13) Correctly through. Trips 14 and 15 were the same.
- (16) Retraced from 9f to 9g 1/2.
- (17) Retraced alley 9f.
- (18) Correctly through.
- (19) 9f 1/2.
- (20) Retraced alley 9f.

Trips 21 to 74 were all correct, and were made with increasing rapidity.

The difficulty persisting from the preceding experience in Bb3 introduced some inhibition for the previously well-coordinated Bb1 movements, a difficulty which centered about a tendency to retrace alley 9f (C) and to stop upon reaching 9c (end of C2). This trouble soon disappeared.

c) *Second change to pattern Bb3* (trip 35, 2/17/27).

February 17

- (35) From food-box to: C2; wandered in the vicinity of C2, and retraced this alley several times. The ant had difficulty in making the 180° turn at A2, causing two returns to the vicinity of alley C.
- (36) C2. There was less wandering, with but two retracings of the alley C2. There were two returns from alley A2 to C.
- (37) Retraced C2 three times, then passed rapidly through to the nest.
- (38) Retraced C2 once.
- (39) C1 1/2.
- (40) The food-box was not reached on the entrance trip.
- (41) C 1/2; C 1/2; rapidly through.

February 18

- (1) Retraced C, then passed to nest.
- (2) C 1/2. Returned to food-box from alley
- 6a. . . . C2 retraced; passed to nest.

Alley C was given primary entrance on all of the above trips, although there was a definite tendency to shorten this entrance.

d) *Second return to pattern Bb1* (2/22/27).

February 22

- (1) 'z' did not reach the food-box on the first trip.
- (2) From food-box to: 9f 1/2; 9g; 9e; 9g; 9e 1/2; 9f; 9d 1/2; 9f 1/10; returned to food-box.
- 9f 1/2; 9f, stopped in corner. Returned to the food-box.
- Slowly passed through the alleys of situation 9, stopping in corners. Alley 9b was retraced, but there were no other errors.
- (3) 9g 1/2; 9f. Ran rapidly after reaching alley 9b.
- (4) Correctly, and rapidly.
- (5) Hesitated slightly at end of 9d, after turning the corner from 9e (C1).
- (6) Trips 6, 7, and 8 were made correctly, and with increasing rapidity.

(9)

Retraced 9f quickly.

Trips 10-16 were made correctly, and with increasing rapidity.

It will be seen that 'z' adapted to this second return to pattern Bb1 much more rapidly and efficiently than she had adjusted to the first.

February 23 (pattern Bb1 remained). There was a slight tendency to hesitate at 9c on two or three of the early trips, but the rest of the fourteen trips were made rapidly and correctly.

March 1. On the first trip, there was a short retracement at the (9e) end of 9f, but the remaining seventeen trips in Bb1 were made rapidly and unhesitatingly.

Although there was a week between the two series of maze trips, the efficiency of the restored Bb1 behavior was not greatly impaired.

e) Third change to pattern Bb3 (trip 19, 3/1/27).

March 1

(19) From food-box to: C2; C; C2; C 1/5; C2; D 1/2; C2; C; D 1/2; C2 1/8; A3; C2; C 1/8. Then 'z' passed rapidly through the remaining alleys to the nest.

(20) C 3/4, D 1/2; C 1/10; A3 2/3; C 1/2; A3; C 1/2; D 1/2. Rapidly to the nest.

(21) C; D 1/2; C. Returned to food-box.
C2; C2; C1; C2; C2; C1; A3; C 1/10.

Passed rapidly to the nest.

(22) A4; C2; C; A4. To food-box.
Passed correctly to the nest. (Seven hour
absence from the maze).

(23) C 1/6. Rapidly to the nest.

(24) C2; D 1/2; D 1/4; C. Passed rapidly to
the nest.

In this record an evident tendency toward the shortening of entrance into alley C may be seen. Figure 8, B, shows the way in which this previously strong habit (the turn into alley 9f from 9g in maze Bb1) was removed on further maze trips. Entrances into the second arm, C2, were quickly checked, although this behavior tended to sporadically reappear at the beginning of one or two further days' trips. Then, after an absence of twenty-

two days from the maze (April 13 to May 5), the old response of turning directly into alley C (9f) reappeared on the earlier trips of May 5, but was eliminated in the course of further trips.

Summary of behavior in situation A4-C, Bb3 (trip to nest). After the first change to the Bb3 pattern, the established tendency to run directly through the alleys of situation 9 persisted as a consistent primary entrance that carried to the end of alley C2. The conditioning effect of this obstruction (C2) is shown by the tendency to hesitate and turn at the end of alley 9d when pattern Bb1 was returned. The serious effects of the interference were soon eliminated, although there was still a tendency to hesitate and stop in alley 9c after the retracing behavior had disappeared. . . . When the Bb3 pattern was returned, although only nine trips were obtained before the next change to Bb1, the experience was not without effect. There was a definite tendency to respond on the Bb1 basis,—proceeding directly to the end of alley C2, crawling about on the wall there, and then wandering. Later, only C, the first arm, was entered. This tendency also began to weaken. . . . When pattern Bb1 was reinstated, there was again the hesitation in 9c, and the retracing in alley 9f. On the first trip after the change this led to three returns to the food-box, but the irregular behavior disappeared much sooner than had been the case for the previous change from the Bb3 pattern to Bb1. . . . Upon the next installment of the Bb3 pattern, the tendency to enter situation C to the end of alley C2 was also seen, but quickly disappeared during the early trips. Its place was taken by a tendency to enter the first arm (C) for only a short distance, and an increasing frequency of primary entrances into the true pathway alternative (A4). At the beginning of a new day in the maze (4/13/27), the primary entrance into C (part way) was more frequent than it had been during the last trips of the preceding day, but these short entrances into C were soon supplanted by consistent direct turning to the true pathway alternative. After a twenty-two day absence from the maze, the first trips in Bb3 again brought a tendency to enter alley C directly from D, but this soon dropped completely, as before. . . . These results show the conflict

that must exist between the alternatives at a junction when each is successively made true pathway by a shifting in maze pattern. In any case, it is clear that a distinct advantage operates in favor of that series of responses which leads into the true pathway, whatever the nature of the maze pattern.

3. *Resumé of results.* A local pattern change that follows the original learning of a maze pattern results in a disorientation which does not involve behavior similar to that found in the primary learning. After the change, there are few incidental, random returns in true pathway, and there is none of the excited behavior characteristic of original pathway saturation. Responses first are made on the established basis, and when this behavior does not carry through the altered situation it suffers gradual elimination as new movements are learned. When disorientation in the changed part of the maze leads the ant to retrace to unchanged alleys, re-orientation occurs there in a fairly prompt manner. The effect of the visual and contact-kinaesthetic controls in maintaining the former efficiency of response in unchanged portions of the maze is indicated by this fact, as well as by the prompt resumption of rapid progress after the altered part of the maze has been passed. Further, the original maze experience definitely aids in the mastery of the changed pattern. The general maze-habituation reduces the possibility of random reversals of direction in open pathway, and tends to limit the commission of errors to the conflict between the old and the new visual and contact-kinaesthetic features of the altered maze.

The errors that occur most consistently and forcefully when the pattern of a learned maze is locally changed are those due to the tendency to respond on the basis of the established sequence of movements. Moreover, the original maze habits persist about in proportion to the strength of the influences operating in favor of their commission in the original pattern. For example, the direct entrance into alley 5 on the trip to food-box through maze Bt1 was strongly favored from the start of learning, while it was only with great difficulty that the turn into alley 9 was established as a part of the trip to food-box through maze Bb1. When

changes in pattern made these turns lead into blind alleys in the respective mazes, the latter turn (into 9) was eliminated with ease, while the turn into alley 5 (B in Bt2) was not completely eliminated by any of the ants in the course of as many as one hundred maze trips. However, the fact that there is always a tendency toward the breaking down of a 'strong' habit, or the restoration of a 'weak' one, when a change in pattern relations makes such an adjustment appropriate to most efficient passage through the situation, shows the great complexity and plasticity of the animal's learned adaptation to conditions.

E. Orientation with reference to the direction of illumination, and adaptation to visual changes

From the time of Bonnet the "finger-experiment" (Section IB) and its easily performed modifications, carried out upon species that characteristically travel upon narrow trails, led discussion to the chemical factor. Consequently, there have been many attempts to explain the total question of orientation by referring to this control alone.

Lubbock and Forel first suggested the importance of vision for the orientation of many varieties of ants. Santschi, Brun, and other later experimenters, have given detailed attention to the function of vision.

The literature suggests two possible ways in which vision may be effective in orientation; namely, through reliance upon differences in intensity of illumination (direction of the strongest rays, light and shadow relationships), and through dependence upon the presence of large objects and other outstanding features of the terrain. The importance of the direction of illumination as a guide in ant orientation has been known since the time of Lubbock. In recent years (1911 on) Santschi and Brun have presented evidence for the latter possibility.

Virtual orientation to the direction of illumination in the learning of a complex situation, a maze pattern, was first investigated by Shepard. Ants were allowed to learn the maze with the light source in a constant position, and observations were made of the results produced by subsequently changing the

direction of illumination. Shepard reported that learning under conditions involving bipolar illumination (light from both sides of the maze) took place less perfectly than did learning with unipolar illumination. Relearning of his maze after a unipolar change in illumination had been introduced required more time than was taken for original learning.

In the writer's experiments, vision could be effective only through orientation to the direction of illumination, since the possibility of adjustment to the position of large objects was carefully controlled. In the report, results will be presented to show the degree of efficiency with which a 90° or a 180° change in the illumination of a previously learned maze can be mastered. Further results will demonstrate the effect of combining illumination from different directions after the maze has been learned with each of the sources separately effective.

1. *Brief survey of experimental conditions (Section I; C, 4).* Figure 2 shows the arrangement of the lighting apparatus. Each battery of four lamps was under the control of a separate switch, making it possible to illuminate either of the two mazes from any one direction or combination of directions by moving one of the transverse inside battery bars to the appropriate position to complete the square of lamp batteries.⁴⁰ This was a necessary feature, since the latter experiments involved relearning of either maze with two opposite batteries illuminating it, two adjacent batteries, or all four of them.

In the main type of visual experiment, before any change in direction of illumination was introduced, the trip from the food-box to the nest must have been learned under conditions involving constant illumination from one direction. As a control, during the visual experiments the light remained in the original position for the trips to food-box, the changes in direction being introduced only for the trips to the nest (i.e., while the ant was in the food-box). (For pattern Bb1, it was necessary to make

⁴⁰ For either maze, the illuminating batteries are designated 'R' (right), 'L' (left), 'N' (nest), and 'F' (food-box). As stated in note 34, these directions are referred from a position at the nest side of the maze. The directions are indicated in figures 4 and 5.

the changes in illumination for the trip to nest before the trip to food-box had become consistently 'errorless'⁴¹ (see note 37).)

The routine exchanges of the true path—blind alley linings at all of the junctions were conducted during all of these experiments, in order to eliminate the differential function of the chemical factor.

2. *The experiments and results.* As before, adapting our method to the conditions of the investigation, we shall present the following cases that have been selected to typify the most important features of the results.

a. *Changing the direction of illumination for maze Bb1.* (Example, ant 'd,' *F. subsericea*). (1) *General course of the experiments.* . . . (see fig. 9).

Ant 'd' was marked on October 14, 1926, and after a four day period in an artificial nest was placed in a maze nest. Her mark, a narrow crosswise strip of white tissue, remained in good condition throughout the ensuing experiments. During her habituation period in the maze, the battery at the *right* was illuminated.

After a few scattered trips on preceding days, the ant completed enough trips (17) on November 8 to attain the standard set for the learning of this maze, enabling the beginning of experiments on vision. On her 18th trip for the day, while she was in the food-box, the first 180° change in illumination was introduced. The following outline presents the course of the further experiments.

November 8, 1926 In 18 trips (including the three required errorless trips), plus five scattered trips on preceding days, 'd' learned Bb1. During the learning, the *R*-battery illuminated the maze.

Change 1) The *L*-battery was illuminated, (180° change), and the maze was relearned in eleven trips.

November 9, 1926 The maze was relearned (*L*-battery) in eight trips.

Change 2) The *R*-battery was illuminated, a 180°

⁴¹ In fact, ant 'd' relearned the trip from the food-box to the nest for all four unipolar changes of illumination, and for two combinations of bipolar illumination, before an advanced stage was attained in the elimination of the three consistent errors (entrance into alleys 4, 6, and 8) made on the trip to food-box through maze Bb1. (Contrast curves A and B, in figure 9.)

change to the original conditions, and the maze was relearned in eight trips.

Change 3) Under bipolar illumination of the two previously learned visual conditions (*R*- and *L*-batteries combined), there was negligible disturbance on the first two trips.

Change 4) Under illumination of the *F*-battery, (90° change), the maze was not completely learned in eight trips, but the last two trips showed only one error each.

November 10-12 Three sporadic trips, under illumination from the *F*-battery.

November 15 The *F*-battery required fourteen trips to be mastered, due to the persistence of one error.

Change 5) Under unipolar illumination from the *N*-battery, the maze was relearned in sixteen trips.

Change 6) The *N*- and *F*-batteries were combined (bipolar illumination). There was only one minor error for each of the first two trips, followed by three errorless runs (see change 3).

(2) *Statement of results for ant 'd.'* Figure 9 offers a graphic presentation of the effects produced by the successive changes in the direction of illumination. The lower curves (A) show the *trip to nest* record, and may be compared with the curves above (B), which shows the record for the *trips to the food-box*, for which run the light remained constant in position. Let us briefly survey the results obtained as the visual changes were successively introduced for the *trips to nest*.

a) *Original learning* (*R*-battery illuminating the maze). Figure 9 shows that the original learning followed the course described on p. 49f. Within ten or eleven trips the maze passage to the nest (after the vicinity of alley 7a was passed) was usually a correct and rapid one. The errors longest to persist for the trip to the nest were due to difficulty in passing the 180° turns in situation 9, but this trouble was eliminated at the fourteenth trip for November 8 (19 trips in all). (It is interesting to note that at that time, although the trips to the nest were uniformly

rapid and without error, the trips to food-box regularly displayed the three errors imposed by centrifugal swing.) The visual experiments were then begun.

b) *Change 1* (180° to the *L*-battery) produced the following outstanding effects in behavior:

When the change was introduced, there was a tendency to maintain the former visual orientation, plainly shown by the persistent wandering along the food-box wall which was furthest from the nest. Similar behavior has been reported by Shepard and by Brun (p. 16f.). The amount of this wandering decreased rapidly during the subsequent trips, having practically disappeared on the sixth trip after the change.

There was difficulty in passing the 180° turns in situation 9 (9e and 9c). This trouble soon disappeared, as a direct result of the 'hugging' (very close contact) of the walls at these turns, a marked feature of the trips following soon after the change in illumination. Shortly after the change was made, the ant usually followed the *F*-wall of alley 9f in close contact, slowed up as the end of this wall was reached, and made a hesitant turn around the corner through 9e, during which the contact with the wall was maintained. The closeness of this contact decreased in time.

Marked hesitancy was observed in the alleys whose passage necessitated progress directly toward the light (in its new position), and particularly in alleys lying closer to the food-box (9f and 9b). The hesitancy in 9f and 9b, and the possibility of ensuing secondary returns to the food-box, persisted for some time. The difficulty at the 9b turn was the last error of all to be eliminated.

There was pronounced hesitancy and a tendency to retrace in the alleys of situation 9, perhaps leading to secondary returns to the food-box. For the most part, after the alleys nearer the food-box had been passed through, there was less tendency to run in a jerky hesitating manner, and to maintain close contact with the inside walls at the turns and at other places along the path, and greater probability of a rapid passage (similar to the behavior effective for these alleys previous to the change).

There was an occasional failure to 'hug' the *N*-wall of either alley 5 or 9 closely enough and in time to make possible the turns into the next true pathway units 3c and 7b, respectively. This was particularly true of the longer alley, 5. (After a time, in eliminating the tendency to over-run into alley 4, 'd' began sooner to come into close contact with

the *N*-wall of alley 5.) In passing through situations 9-8 and 7-6 this difficulty was not as marked, since in these alleys, after the speed of running had begun to increase on further trips, centrifugal swing was effective in aiding the appropriate contact.

Twenty-four hours after the first change, the ant had little difficulty in relearning the same situation. There were some signs of a tendency to commit former errors, yet the only trouble occurred on the first two trips, and was due to difficulty in making the 180° turns at 9e and 9c, and to a recurrence of the tendency to over-run into alley 4.

c) *Change 2* (return to the *R*-battery, a 180° change).

On the first trips the ant had difficulty in making the 180° turns 9e and 9c, a feature that rapidly disappeared.

d) *Change 3* (combination of the *R*- and *L*-batteries).

The ant was not noticeably disturbed on leaving the food-box, although there was a very short over-run into alley 4. This error occurred on each of the two trips following the change, but there was a prompt recovery and turn into alley 3c in each case. This was the only error produced by the change.

e) *Change 4* (a 90° change to the *F*-battery).

The difficulty at the 180° turns (9e and 9c) was soon supplanted by a 'hugging' of the inside walls at these turns, which enabled an increasingly rapid passage through them.

There was a tendency to over-run the entrances to alleys 7c and 3d, into alleys 8 and 4 respectively, and this was especially true of the latter. Soon, by a close 'hugging' of the near wall (i.e., the *N*-wall of 5) of the approach alley through a short distance preceding the turn, the difficulty was eliminated. When over-running did occur, the return was promptly made, after a short entrance into the blind alley, and the recovery was characterized by close hugging of the near side (*N*-wall of 4) of the blind alley.

As before, the alleys near the food-box were run through more slowly on the trips made just following the change.

After an interval of six days, there was a reappearance of the characteristic difficulties on the first trip, with a rapid increase in efficiency on further trips.

f) *Change 5* (to the *N*-battery).

The main difficulty was again in the alleys of situation 9, the progress being more rapid and correct after alley 7b was entered, and increasingly

so as the nest was approached. In 9e and 9c the 180° turns led to some hesitation and initial retraceals.

There was hesitation in the alleys which involved passage directly toward the light in its new position,—in 9g and 9a, especially, and in 7b, and to a slight extent in 5a and 3c. This hesitation would appear immediately after the turn into the alley, and during early trips was usually followed by a retraceal.

In passing through alley 5, there was an interesting tendency to run closer to the *F*-wall as soon as the direct influence of centrifugal swing permitted it. Hence, for the first few trips there occurred an over-running for a short distance into alley 4.

On trip 33, 'd' stopped in the 9f-g corner before the food-box was reached (illumination from the *R*-battery, therefore), and picked up a piece of food dropped by another ant. She then turned around rather promptly, without passing to the food-box, and proceeded back through the maze with but one minor error. This behavior was frequently observed in other ants.

g) *Change 6* (combination of the *N*- and *F*-batteries).

There was no difficulty other than a slight over-running of the entrance of alley 7b (entering alley 6) on the first trip, and the entrance of alley 3c on the second (running into alley 4). This behavior was characterized by a prompt recovery, as usual. (cf. change 3.)

(3) *Brief resumé of the results for ant 'd.'* Maze Bb1 was relearned under conditions successively involving a 180° change in direction of illumination from the original position, a return to the original direction, and a combination of these two directions in the same situation; then a 90° change, a further shift to the direction opposite this, and a combination of these two visual conditions. The results show that after the maze has been learned with constant unipolar illumination, it can be relearned under conditions involving illumination from the other main quarters, separately or in combinations of two.

In the case of any change in direction of illumination, (excepting the combination of previously learned situations), there are characteristic errors that appear with respect to certain pattern features. Visual changes introduced while the subject is in the food-box (before the trip to nest) produce hesitancy and errors

which are mainly localized in alleys of the maze lying near the food-box. The alleys lying closer to the nest are passed through rapidly and with an efficiency that is not much less than that established before the change. Further, the introduction of the various changes in direction of illumination for the trip from food-box to nest has no noticeable influence upon the trip in the opposite direction, under the conditions of these experiments (see note 41).

b. *Experiments involving more complicated changes in the direction of illumination (trip to nest, maze Bt1—Example, ant 'omega,' F. subsericea).* The sample records presented in the preceding section show that a *Formica* ant can adjust to many successive changes in the direction of a single source of illumination, but we have not yet seen the most complicated type of visual situation the ants are capable of mastering. We shall consider a further case representing experiments in which learned visual conditions were reintroduced, combined and recombined, and alternated one with another in many ways, meeting with successful adjustment in every instance.

(1) *Relearning of situations involving alternate illumination from two unipolar sources.* The following results were obtained by means of a procedure which involved the alternate introduction of the source which had illuminated the maze during original learning and illumination from a new quarter of the maze. Each trip made under the new visual condition was followed by three during which the maze was illuminated from the original direction.

a) *Conditions.* On May 7, 1926, 'omega' demonstrated her mastery of maze Bt1 by making five trips which involved no errors for the trips to nest and but one error each (partial entrances into alley 6) for the first two trips to the food-box. On trip 15 for this day, while the ant was in the food-box, the light was switched from the *L*-battery, which was effective during original learning, to the *F*-battery (90° change). During the following fifteen trips, the two batteries were alternately introduced for the trips to nest (the changes being made each time after the ant reached the food-box).

b) *Results.*

TRIP	DIRECTION OF LIGHT	BEHAVIOR	TIME
15	F (new)	The ant wandered about the food-box, especially near the left side. She finally entered alley 7d, hesitantly, and proceeded slowly through the alleys of situation 7, hugging the alley walls closely. She passed into alley 6 hesitantly, and hugged the L-wall in leaving alley 6, thus passing directly into alley 5e. She hesitated at 5a, and passed through alley 5 wandering from side to side, thus entering 3d directly. Passing very slowly but correctly into 3d, she went slowly through 3a (toward light), showing a periodical tendency to quicken her pace. The ant retraced 3, then over-ran into 2a. She seemed temporarily disoriented, but quickly recovered, to pass from the maze and down the bridge.	2'50"
16	L (old)	There was some hesitation in making turns, particularly in alleys near the food-box. The trip was otherwise rapid and correct.	35"
17	L (old)	Less hesitation was observed, but there was a slowing up in passing through alley 3c, apparently due to the fact that another ant occupied the center of the alley.	40"
18	F	'Omega' wandered about the food-box, mainly on the left side, as on trip 15. She returned from alley 7a 1/2 to the food-box, first dropping her food in the corner at 7c, retracing 7b and recovering the food, and retracing alley 7a twice. Then she left the food-box, slowly passing through the alleys of situation 7, stopping once or twice at 90° turns. She picked up speed on reaching alley 5d, but hesitated in alley 5b, experiencing some difficulty in making the 180° turn there. Running down the center of alley 5, the ant passed into 4, but turned at once on coming to the end of the exchanged lining (4 3/4). Passing back to 5 4/5, she veered sharply to the L-wall of 5, and hugged this in a rapid course through alley 5 and into 3d. She rapidly ran through the rest of the maze.	2'40"
19	L	There was a partial retraceal of alley 7 (7 1/2), after a slight hesitancy in passing through the other alleys of situation 7, but otherwise 'omega' passed quite rapidly through the maze to the nest.	43"

TRIP	DIRECTION OF LIGHT	BEHAVIOR	TIME
20	<i>L</i>	The ant slowly passed through the alleys of situation 7, and slowed up somewhat before turning into 3d. Excepting this, her course was rapid and correct.	42''
21	<i>L</i>	The run was rapidly made, except for a slowing up in passing through alley 5.	47''
22	<i>F</i>	The only error was the over-running into alley 6 1/2, with a rapid return and entrance into alley 5e. There was also some hesitancy in making the turns in situation 5, and in passing through alley 5b.	47''
23	<i>L</i>	Her pace quickened considerably as the nest was approached, and the previous slight hesitancy was not observed in the alleys of situation 7. She dropped her food while passing hurriedly through alley 5b (180° turn and ran on into alley 5a a short distance, but then quickly turned around, picked up the food, and continued rapidly to the nest.	48''
24	<i>L</i>	' <i>Omega</i> ' over-ran into alley 2 1/5 (the first time she had done this), but turned around at once, and passed rapidly through alley 1.	45''
25	<i>L</i>	Passed somewhat more slowly through the alleys of situation 7, but went very rapidly after entering alley 5e.	38''
26	<i>F</i>	Ran to <i>L</i> -side of the food-box when the illumination was changed, but turned away at once. She passed through the maze correctly, though somewhat hesitant in her progress through alleys near the food-box.	45''
27	<i>L</i>	Moved much faster, without hesitation.	34''
28	<i>L</i>	Over-ran into 4 1/2, but her return and entrance into 3d was rapidly performed.	43''
29	<i>F</i>	' <i>Omega</i> ' bumped into the wall at the 180° turn through alley 5b, which caused her to retrace alley 5c 1/4, but she then turned around quickly and passed rapidly toward the nest. Further alternations of the visual conditions brought no disturbance; all trips were rapid and correct, whether the <i>L</i> or the <i>F</i> -battery was introduced.	42''

c) *Brief summary and discussion.* Comparing these results with those obtained from experiments in which the change in illumination persisted until learned, we find that *an evident advan-*

tage is gained by the alternation of the new condition of illumination with the old and thoroughly learned one. In cases where alternation of the visual conditions was not performed, the errors introduced by the changed illumination tended to persist for some time, and were eliminated very slowly. In contrast, when the habituated visual condition was regularly reintroduced, the primary disturbance rapidly disappeared in favor of the responses characteristic of the well-learned behavior.

Apparently, the more often the visual situation changes, the greater is the reliance upon those features which remain constant. However, our results indicate that when the visual change remains in effect until learned, the altered condition somehow prevents the unchanged features from exercising their established control. On the other hand, the more rapid elimination of the errors when the original and new visual situations are alternated points to the possibility that the ant derives some benefit from the interspersed runs made under the earlier visual condition. The writer believes that the advantage rests in a contact-kinaesthetic control which is less effectively inhibited by the new visual features when they do not exert a steady and cumulative influence upon it.

This process of transfer seems to operate in the other direction, as well, since there is evidence that the alternation procedure serves to introduce a measure of uncoördination to the trips made under the learned visual conditions. Thus, when *L*-illumination was alternated with trips under *F*-illumination, in the former case there appeared some hesitation in alley units near the food-box, and other characteristic errors ordinarily produced by the introduction of a visual change.

(2) *Alternations and combinations of the four directions of illumination.* The following group of experiments was conducted after 'omega' had learned the maze under conditions involving the four unipolar sources of illumination, successively introduced and each persisting until mastered. On May 14, as a check upon the learning, an experiment was conducted which involved a change in illumination for each trip, alternating among the four possibilities. The successive changes failed to produce

any disturbance or disorientation, other than a slight tendency to hesitate in passing through the alleys near the food-box. The next step in the procedure was to institute conditions involving combinations of the batteries, and these experiments will be briefly reviewed.

a) Illumination from the R- and L-batteries, separately and in combination. It was first ascertained that there was no disturbance when the maze was illuminated by either of the batteries alone. Then the two were combined into one (bipolar) situation, and orientation was not disturbed in any way (cf. changes 3 and 6, p. 101f.). Then the following tests were conducted:

*I—L-battery alone—*No change in behavior.

*R-battery alone—*No change in behavior.

*II—L- and R-batteries combined (bipolar)—*On each of the first four trips there was a minor error due to some difficulty in situation 6-7, or to hesitancy in an alley near the food-box. In other respects, the behavior was as before, and the last three trips were rapid and efficient.

*III—L-battery alone—*On the first trip the only error was a return in alley 5c, apparently due to difficulty in proceeding toward the light through this alley. The two following trips were rapid and without errors.

*IV—R-battery alone—*There was a return from 5b to junction 6-7 on the first trip, due to difficulty at the 180° turn in 5b. There were no other effects on this trip, and the two following trips were correctly made.

*V—L- and R-batteries combined—*The second of four trips involved a rapid return from alley 7c 1/4 to the food-box, but the passages were otherwise efficient and rapid.

*VI—L-battery alone—*Rapid and errorless trips.

*R-battery alone—*Rapid and errorless trips.

A repetition of the above experiment, next performed for the *N-* and *F-* batteries, produced results that were substantially the same.

b) Illumination alternately from all four batteries, two opposite or adjacent batteries, or from separate batteries.

*I—*All four batteries combined—After illumination from the separate batteries, or from two opposite batteries in combination, had pro-

duced no observable disturbance, the introduction of all four into the same situation (*universal illumination*) brought no errors during three trips to the nest.

II—Re-introduction of the universal illumination on the first trips of the following day brought only a tendency to hesitate and turn slightly at junctions 4-5 and 6-7. Occurring on the first three trips, this difficulty was plainly due to the first exchanges in linings at these junctions, and not to the light. The trips were otherwise rapid and correct.

III—*L*-battery alone—Three perfect trips. After an interval of four hours absence from the maze, there were two additional rapid and correct trips.

IV—All four batteries combined—The first trip was rapid and efficient, with the exception of three short retraceals at junction 4-5. On the next eight trips there was an average of one minor error each, usually a hesitation or minor retraceal at a junction or in an alley of situation 7. Otherwise, these trips were correctly made. This result is uniform for experiments involving the introduction of universal illumination directly after trips for which a single battery has illuminated the maze. There is usually less disturbance if the universal illumination follows two or three batteries in combination.

V—On the same day, illumination from the *L*-battery, then from the *R*-battery, and next from the *L*- and *R*-batteries in combination, gave uniform rapid and efficient successions of two trips each.

VI—*L*- and *F*-batteries, separately and combined—The introduction of these previously learned batteries separately and in combination produced results that are quite in agreement with those similar experiments performed for opposite sources (changes *III* and *V* above). Hence the lack of disturbance in combining previously mastered conditions of unipolar illumination into new bipolar situations is true of the combination of adjacent as well as of opposite sources.

(3) *Brief discussion of the results obtained for ant 'omega,' as an example of adaptation to changing visual conditions.* Our earlier visual experiments showed *F. subsericea* individuals able to habituate to each of the four sources of illumination in turn (one battery illuminating the maze until mastered). Were it not for the fact that correct orientation and rapid progress are quickly restored after the introduction of illumination from two, three, or four quarters of the maze, one would consider the above

performance not more than a matter of developing an ability to change readily from one visual-motor system to another.

The results of the present section indicate that a control of orientation by the visual features of the different situations must be very plastic. But it cannot be held that the described performance is based entirely (or mainly) upon the development of a separate system of responses for each of the visual conditions,—not in the face of the fact that the combination of the separate visual situations fails in every case to interfere with passage through the maze. An examination of these and other results suggests that the plastic adjustment represents a growing independence (which does not mean absolute independence!) from the direction of illumination as an orienting factor. Apparently, the reliance upon other controlling factors becomes correspondingly greater when the visual control is made unstable, and particularly when visual differences do not exist (universal illumination).

It is our conclusion, then, that the ability to pass to the nest through the maze under any one of two or more visual conditions taken alone, and to adjust to the interchange of these conditions from one trip to the next, is not merely a matter of a separate series of integrative relationships for the contact-kinaesthetic and visual features peculiar to each situation. It must mean an ability to become relatively independent of vision, in favor of the basic and unchanged contact-kinaesthetic control. The following example of other experiments is of some significance for this discussion.

An ant (*F. subsericea*) labelled '*delta*' learned the trip to nest through Bb1, the *F*- and *N*-batteries being alternated every five trips. Following original learning, the visual conditions were alternated for three groups of two trips each, and finally, for seven trips during which a change was made each time. In the latter case, there was a consistent absence of disorientation. . . . This seems to indicate that if one does not wish to make maze-running a matter of independence of the light, the variations in its direction should not occur often during the trips. Frequent alternation of the visual conditions leads to greater independence of their control.

The above discussion far from denies the fact that orientation will occur on the basis of a constant difference in illumination, when such a difference exists. All of our experiments dealing with visual changes that directly follow the learning of a maze (under constant illumination) bear out the statement. However, as the number and frequency of changes in direction of illumination increases, we have found the resulting disturbance and disorientation to decrease, which suggests the point we have made.

Summing up, the direction of rays is effective whenever its differential aspect is marked enough, but when this is not the case, the other factors apparently become more important in the control of orientation. The more often the direction of illumination is changed, the less reliable it becomes as an orienting factor, and the more the unchanged features are depended upon. Since in our experiments the possibility of differential control on the part of the chemical factor was eliminated, the remaining possibility is the contact-kinaesthetic factor.⁴²

c. Experiments on visual and contact-kinaesthetic control. The importance of the direction of illumination is further shown by tests that involve a visual change which is introduced while the ant is passing through a maze alley (after learning has taken place under constant visual conditions). Shepard, in performing this experiment, reported a uniform tendency to turn and retrace the path, then to wander.⁴³ Santschi obtained substantially the same results for his mirror-experiment conducted in the open.

⁴² Observation of maze behavior (following a change in the direction of illumination) bears out this statement in many ways. Most of the disorientation occurs in the alleys near the food-box. As the ant progresses further through the maze, her speed increases, and her behavior more closely resembles that seen before the change was introduced. Again, the walls of alleys near the food-box are followed in close contact, a feature which disappears as the ant's pace begins to quicken. Then too, any influence (180° turn, artificial interference with progress) that causes the ant to slow up in passing through the maze alleys tends to introduce disorientation.

⁴³ Shepard also reports other strong indications of virtual orientation to the direction of the controlling light source; among them the fact that, after the ant has learned the maze under constant conditions of illumination, she may be "led all over the maze" by appropriately moving the light. The apparent solution for this fact is that the pattern of Shepard's maze (p. 24f.) necessitates the maintenance of one bodily position, with reference to the light, much more consistently than any other.

The experiment may be employed to demonstrate not only visual control, but integrative control of orientation, as well. This can be done by appropriately introducing the changes in illumination according to the pattern features of the maze. The following case is representative.

(1) *The experiment (a 180° change in direction of illumination introduced during passage through maze Bb1) and results*

Ant 'y', *F. subsericea*, learned maze Bb1 under constant illumination furnished by the *L*-battery. On a subsequent trip (just after the standard had been attained), the direction of illumination was shifted 180° to the *R*-battery when the ant was half-way through alley 5b (returning to the nest).

The ant stopped abruptly after running a short distance in the original direction, ran onto the alley wall, and then turned back to run through the portion of alley 5b just passed. She turned directly into alley 6, and ran rapidly through this alley. The turn into alley 6a was also rapid, as was the passage to the end of the alley. Upon running into the end wall of alley 6a, the ant responded by crawling persistently about the wall, and especially on its *F*-side. Finally she resorted to repeated returns in alley 6a, and wandered to alley 8a, where she roamed about in the vicinity of situation 8-9.

While 'y' was in alley 8 the illumination was shifted 180° to the original condition (*L*-battery). She passed somewhat slowly into alley 7b from 8, but near the end of 7b her pace quickened, and she ran through the rest of the maze quite rapidly and efficiently. However, there was a slight hesitancy in alley 5b, again seen on the next two trips (to the nest), but not thereafter.

This experiment was repeated under the same conditions for four other ants of this species, after each of them had learned the maze with the *L*-battery illuminating it. In each case, the reversing of the direction of illumination led to results that were quite the same as those described, up to the behavior at the end of alley 6a. A similar result was obtained, when later, for two of these ants, the light was reversed 180° (*L*- to *R*-battery) during the passage through alley 9 (*trip to nest*). Here, as before, the direction of progress was reversed promptly, and there was a return to alley 9a, a rapid turn into 9b, and rapid passage through this alley. Difficulty ensued in alley 9c, involving crawling about, especially near the *N*-side, before the final wandering began.

As a control test, the light was reversed 180° during passage through

the central part of alley 3b (trip to nest), on different occasions for ants of this group. In each case, the result was a prompt 180° reversal of progress, and a direct passage through alley 3b toward 3c, followed by repeated crawling about the corner between these alleys, and by wandering.

(2) *Discussion.* Examination of the pathway details in figure 4 will show that progress through the succession of alleys 5b 1/2 to 6 to 6a involves a series of turns that is entirely similar to the 5b to 5a to 5 succession. With illumination from the left side of the maze, progress through the 5b 1/2-5a-5 alley sequence necessitates the following course: passing toward the light (through 5b), turning to place the light on the right (into 5a), running along this alley with the light on the right, turning to run (through 5) away from the light, and then turning in response to certain stimuli (p. 74ff.) to run through a further alley (3d) with the light at the right. With illumination from the right side, this description holds for the passage from alley 5b 1/2 to the end of 6a. Hence, on their face these results can be accounted for by assuming that the ant had learned to make a series of turns with respect to the direction of illumination.

The experiments involving introduction of the 180° change as the ant was passing through the central part of alley 9 gave results that indicate a similar state of affairs. Here also, it may be assumed that the ant tended to retain her learned position with respect to the light, and to change this in the original sequence, beginning to wander when her reversed course required dissimilar turns. This is suggested by the fact that whenever the light was returned to its original position, progress toward the nest was resumed after a short time (in which one or two turns of the original alley series were run through slowly).

However, this explanation is not a complete one. The behavior following the reversal of illumination was not similar to the original behavior merely because the visual conditions were the same with respect to a succession of alleys, but also because the duplication of the original alley-sequence permitted the contact-kinaesthetic control to function as before. In every case, the progress from 5b 1/2 to the end of alley 6a, or from 9 1/2 to the

end of alley 9b, after the light was reversed, involved the detailed behavior characteristic of the respective original conditions,—turning movements were the same, contact with walls occurred in much the same way and at corresponding places, etc. Further, by lengthening or shortening the alleys of the reversed sequence (chemical factor controlled) in a situation similar to the above, the writer has been able to show that the smooth performance of the movement-sequence does not occur when the light is turned through 180°. Here, although the relationship of the illumination and the successive turns remains the same, the duplicated sequence is not followed out to any extent.

d. The control experiments. Many experiments were performed to test the special characteristics of visual control. The following sample presents some interesting features.

(1) *Experiment (90° change in illumination, following original learning).*

Conditions: Ant 'z' learned Bb1 so that on the ten trips preceding the visual change (see Appendix I, and Fig. 7) the trip to nest had been made rapidly and efficiently. On her 63rd trip for January 17, while she was in the food-box, the battery of lights at the right side of the maze (effective during original learning) was switched off and the *N*-battery illuminated.

Results: (Ant 'z' reached the food-box, and the illumination was shifted 90°). The ant went to the left wall of the food-box, to wander about this side for some time. Finally, in her wandering, she hit upon the entrance to 9g and went half-way through this alley, but then returned to the food-box, where she wandered near the left side. Again 9b was entered; this time 'z' proceeded to alley 9e, with noticeable general hesitation in course. Unable to make the 180° turn, the ant retraced, after persistent contact with the *F*-wall of 9e. She went back through 9f, hesitating at the corner; then returned to 9e, after having some difficulty getting into alley 9d. There was considerable trouble, involving some retracing, before she passed the 9c turn. Passing through alley 9a, 'z' returned to 9b 1/10, and then hurried back, hugging the *N*-wall of 9 in going to 7b. Now her pace quickened, and she passed correctly and rapidly through situation 7, but she did not come into proper contact with the *L*-wall of alley 7, and so over-ran into alley 6. Then she retraced slightly at the end of alley 6a, and 6a 4/5 was

retraced at its end. This behavior was repeated, after which the ant turned to proceed more rapidly from the alley, hugging the *L*-wall of alley 6, and thus getting into 5b. However, there was very evident difficulty in passing directly toward the light in alley 5a. This produced a return to 5b 1/2, thence to 7, and back to 5a, where the trouble re-occurred. After passing to 6a, she returned to 5a, but again failed to pass, and she again passed to 6a, coming back to 5a, but failing to get through, as before. (In returning from 5a to 6a, she hugged the *L*-wall of 5a each time, crawling on the *F*-wall of 5b, and of necessity turning into 6a). Now she passed to alley 7, directly through alley 7 to 9, to 9b 1/10, retracing 9b, and thence passed to the food-box. (Out 3' 30".) She passed out again at once, after returning from 9g 1/3 end to 9e. She passed to alley 5a (contact with *F*-wall of 9d, with *N*-wall of 9, and thus the *L*-wall of 7), but retraced this alley, crawling on the glass, and reached 6a. She then ran about in this vicinity:—5b 2/3 to 5b 1/2, 5a, 5 1/2 end, 5b 1/4, 5a 1/2; 6a 1/2, 6a. Then she rapidly ran to alley 8, to 9b 1/10, 9 1/8, 9e, 9c, and 9e. Passing out more rapidly, and hugging the *N*-wall of alley 9, 'z' again proceeded to 5a, but had the same difficulty there:—5a 1/6 end, to 6a, to 5a 9/10 end, to 6a, 6a; back to 5a; to 6a, 6 1/8 end; and again back to 5a. Now she crawled on the glass at the junction 6-7, dropping the food which she had carried up to that time. Proceeding to 9b 1/10, she retraced to 9a, thence to 9c, 9d, 9c, and returned to 9b, crawling on the glass, then retracing 9b, 9c, 9b, and again in 9c. Passing rapidly through alley 9, the ant over-ran into alley 6, and wandered to 6a, 6a, and thence to 5a, where she hesitated. She returned relatively rapidly to alley 9c. After wandering to 9, she made one or two partial retracements of that alley, and then proceeded to the end of 8a, from 8 1/6 end back to 8a, and passed from alley 8 on the glass. Entering 7b, she quickly turned to pass through situation 9, returning through 9c before passing to the food-box. She had wandered seventeen minutes in all, after the change in illumination was made.

The illumination was again shifted 180° (to the *R*-battery, the original condition). 'z' had been wandering about the food-box, but upon the change of the light she required little time to leave. Though without food, she passed through the maze alleys rapidly and correctly, notwithstanding some hesitation in passing through the alleys of situation 9. She hesitated upon entering alley 5a, returning from the end of 5a to 5b 1/8, rather rapidly, and hesitated again on returning to 5a, but proceeded rapidly through the remaining alleys of the maze to the nest.

On the next trip, number 64 for the day, *the 180° change was again made* while 'z' was in the food-box. She passed to the *L*-wall of the food-box, as before, and soon hesitantly passed to 9b 1/10, thence to 9f 1/3, 9d 1/6, and back to the food-box. Leaving at once, the ant went to 9c, stopped in the corner of alley 9, passed on the *N*-wall to 7 and hence directly into 7b, going rapidly through the alleys of situation 7. She hesitated after entering alley 5a a short distance. Retracing to 5b, she then returned to pass hesitantly through 5a, and took a meandering course through alley 5, thus passing into 4 1/5, but returning correctly to pass into alley 3c. Running rapidly through the alleys of situation 3, 'z' over-ran into alley 2a, thence wandering back to 3a 1/10. Here she turned rapidly to pass back to alley 3, but again over-ran into alley 2a. Once more she retraced to the end of 3a, back into 2a, and then turned to proceed rapidly toward the food-box. Entering alley 6a, she returned to 5a 1/2, then ran to 5 5/6, retracing somewhat in alley 5, entered 4. Turning, the ant passed back rapidly through the alleys of situation 5, but entered alley 6. Retracing from 7 1/4 to 5b, she then turned and quickly passed to alley 9b. Stopping in the corner of 9 for a time, cleaning her antennae, she then crawled through the alleys of situation 9 to the food-box. She had been in the maze for 5'05", and had retained the piece of food throughout the course of her wandering.

While 'z' was in the food-box, the *light was returned to the right side* (original condition). 'z', crawling about on the *L*-wall of the food-box, at once left the food-box, and proceeded fairly rapidly through the alleys of situation 9. With some hesitancy in alley 5a, and a return from 5a to 5b 1/2, she passed rapidly through the maze to the nest.

(2) *Discussion.* This is an example of the various brief control experiments, all of which demonstrated from one or another angle the importance and necessity of the light rays as controllers of responses in normal maze-orientation.

It should be noticed that the change of illumination introduced directly after original learning was through an angle of 90°, rather than through 180°. The latter condition was effective for all of the more detailed visual experiments. Although there were only three control experiments involving a change through 90° after learning had taken place, the results seem to indicate that there is a more radical disturbance and disorientation when the first

change is made to an adjacent battery, than when the illumination is reversed through 180°.

There are important individual differences in the responses of ants to changes in the direction of illumination, as shown by the main visual experiments and the controls. As Shepard reports, the rapidly moving ants seem to be disturbed less by the visual changes than do the slower travellers. Ant 'z' was of the former type, and yet the changes in illumination caused her to wander for some time without getting through the maze. However, the difficulty was mainly based upon the inability to pass toward the light through alley 5a. Due to the influence of such crucial errors, the disturbance resulting from a change in the direction of illumination is often greatly exaggerated.

It is interesting to note the prompt recovery that occurred when the original conditions of illumination were restored. Although the ant had some difficulty in passing slowly through the alleys near the food-box, and although the influence of the trouble in alley 5a was to be seen (conditioned hesitation), the general rapidity and efficiency of her movements was characteristic of the integrative sensory control established during original learning.

F. General summary of results

1. The principal experiments were performed with *Formica subsericea* and *Formica exsectoides* (see note 14), two species standing high in the family *Formicidae*. The ants were kept in the laboratory, in permanent earth-filled nests. The nest in use was connected with the maze by a bridge, and in the experiments the worker ants were allowed to pass through the maze to get food, and to return through the maze to the nest with the burden. Maze patterns *A* (*A1*), *Bt1* with its modification *Bt2*, and *Bb1* with pattern modifications *Bb2* and *Bb3* (see Figs. 3, 4, and 5, respectively) were used. Studies were made of the principal factors effective in controlling orienting behavior, and of the ability of ants to learn new maze patterns, or to adapt to changes in the situation (maze pattern, direction of illumination).

2. *Significance of the chemical factor:* In their field orientation the *Formica* species characteristically pass over thoroughfares (across an area, without superimposition of single trails). Various experimenters

have shown that under these conditions the chemical traces are not laid down in a manner that permits them to guide orientation. Yet whenever a number of trips are made by any one ant over a relatively restricted ("canalized") path, the chemical substances on the path may become of significance in guiding the ant. Hence the chemical factor must be taken into account in maze studies.

By lining the maze with bristol board units that covered the floor and walls of the alleys (Shepard's method), it was possible to control and study the influence of chemical stimuli. There is a slight polarization (end-to-end difference, qualitative or quantitative, or both) in the maze trail, since the exchange of pathway linings from widely separated alleys produces a minor disturbance. However, as Shepard found, there is no evidence that a pathway polarization is of guiding significance in maze learning.

Shepard proved that at the crucial places in the maze (junctions of true pathway and blind alleys) the chemical features will guide the ants if the pathway is not disturbed during learning. In the writer's experiments, by regularly exchanging the adjacent true pathway and blind alley linings at junctions (pp. 35, 42f.), it was possible to effectively eliminate the differential effect of the chemical factor,—i.e., turning movements could not be made on the basis of utilizable chemical differences between the alternatives. This was shown by the fact that after three or four exchanges of the linings had been made at a junction during the early course of learning, further exchanges had no effect on behavior. However, there was some tendency for the first lining exchanges of a new day's runs to bring a short-lived return of the disturbance.

3. Many *F. subsericea* ants were able to learn the rather complicated maze A pattern (Fig. 3), which involved ten blind alleys. *F. subsericea* and *F. exsectoides* ants readily mastered the Bb and Bt patterns (Figs. 4 and 5), which were used in the principal experiments.

For all of the experiments reported in this paper, the routine exchange of adjacent true path—blind alley linings was effective. This, as we have said, was done to eliminate the differential effect of chemical substances on the pathway. Learning took place more rapidly when no exchanges of linings were performed, and when the pathway linings remained in place until the maze was mastered.

Observations of behavior during the early maze trips of an ant show a tendency toward somewhat irregular activities, with more than one possible return to the beginning before the food-box is reached, and with several returns from parts of the maze to the food-box before the nest is

regained. The first sporadic and irregular errors are rapidly eliminated, leaving those that are more firmly based upon the pattern features of the maze.

The error and time curves for ant learning of the maze typically follow a course that is best described as 'negatively accelerated.' In considering the results of these experiments, the trips through the maze in the two directions (to food-box, and to the nest) have been treated as separate cases. The curves (error or time curves,—Fig. 6) drawn to represent the course of original learning for the 'trips to food-box' and 'trips to nest' show about the same rate of decline, although the similarity does not apply to the specific features.

4. Our results are quite in agreement with those of Shepard, in showing that there is little decrement in maze-running efficiency due to non-practise over a considerable interval, after the maze has once been learned. After periods as long as three weeks (under conditions involving the routine exchange of pathway linings at the junctions), ants showed surprisingly little decrease in efficiency of running when the maze passages were resumed, and there was prompt return to the former standard in most cases.

On the whole, *Formica subsericea* ants were superior to *Formica exsectoides* in learning the maze. A *subsericea* individual was much more likely to complete a large number of consecutive maze trips than was an *exsectoides* ant. This rendered *F. subsericea* ants better subjects for the maze experiments, and for that reason most of the discussion centers around the maze behavior of this species. However, the fundamental results that are reported for the maze-learning of *F. subsericea* also hold for *F. exsectoides*.

There were evident individual differences among the ants in their maze-behavior, and in their learning ability. The maze-behavior of a single individual was also found to vary at different times, as shown by the sample case report (Appendix I, Fig. 7).

5. Experiments were conducted which demonstrated the ability of ants rapidly to improve the efficiency of their maze-running, when over a number of initial trips the food was found each time in a different maze alley, and a greater number of alleys must be passed through to obtain it. In an experiment involving the finding of food in this manner, ants were able to decrease the number of committed errors, and to increase the smoothness and rapidity of their progress through the maze alleys (p. 55f.).

6. *Centrifugal swing* (Section II; C2): By appropriately planning

the pattern, an ant maze may be made easy or difficult, although the number of blind alleys remains the same. This fact is mainly dependent upon the centrifugal swing principle, which is very important in maze-orientation and learning, and especially so in its close relationship with the contact and kinaesthetic factors (pp. 66-71). We have applied the term *centrifugal swing* to the fact that if two successive turns are made toward the same side (i.e., both toward the right or toward the left side) through appropriately situated maze alleys, the momentum gained by the ant will throw her into close contact with the outside wall (note 33, p. 69) of the last alley in the series, and the next turn will tend to be toward the side of this contact. This is very important in determining the contact- and kinaesthetic-motor relationships that develop during maze-learning.

For example, maze *Bb1* was designed with three blind alleys the entrance into which was favored by centrifugal swing on the trip to the food-box (*type 1 blind alley*). On the trip to the nest, however, the entrance into these alleys was opposed on the same basis (*type 2 blind alley*), and entrance into the true pathway alternative was favored in each case. As a result, all of the ants regularly entered the *type 1* blind alleys from the start of learning (Table III, alleys 4, 6, and 8, trip to food-box), whereas *type 2* (Table II: alley 4, trip to food-box; of Table III, alleys 8, 6, and 4, trip to nest) was quite the opposite. Hence, even the first trip through the maze can scarcely be termed 'random' in nature.

7. *The elimination of the tendency to enter blind alleys.* Although passage into the *type 1* blind alley becomes a consistent part of the maze-behavior of any ant, and continues thus for some time, with further trips there are always important changes in this behavior. If the alley has two arms, the second arm will not be entered after the first few maze trips (p. 58), and the ant will retrace immediately upon contact with the wall at the end of the first alley. The second arm is usually not eliminated by degrees, but as a whole. In the course of this elimination, the full length entrance alternates with a tendency to turn around directly upon contact with the end of the first arm, and rapidly becomes less frequent than the latter.

The elimination of the tendency to enter the first arm of a *type 1* blind alley uniformly progresses very slowly (pp. 58-62) and Fig. 8). In time, behavior involving full length entrance and a return upon contact with the end of the alley alternates with a rapidly growing tendency to turn back promptly after having entered the alley but a

short distance. The latter behavior gradually predominates, and in time alternates with an increasing tendency to turn directly into the true pathway without entering the blind alley at all. For all ants, a great number of maze trips was required to attain a relatively advanced stage in the elimination of the 'favored' *type 1* blind alleys. In contrast to this, the *type 2* blind alley was always eliminated with great facility.

We have analyzed the blind alley—true path situations in the two mazes used in the present experiments, considering the results for the trips to the food-box and to the nest in each case (pp. 71–73, Tables 2 and 3). All of the studies have shown the centrifugal swing principle a powerful factor in determining the course of learning and of relearning.

8. *The importance of kinaesthetic control of maze behavior:* The results indicate that as learning progresses the kinaesthetic control of movements made in passing through the maze takes on an increasing importance. In addition to the reports given in this paper, the writer has found that experiments involving the lengthening and shortening of true path units after the maze has been learned bring results that throw the kinaesthetic influence into relief. When sections of true pathway are secondarily lengthened after original learning, the ant tends to turn where the alley opening originally was located, or when the alley is secondarily shortened, the ant usually runs violently into the wall at its end, and is very much disturbed. This shows that the kinaesthetic stimulus, or rather, the configuration of stimuli, brought by the attainment of a certain stage in a series of movements, after learning has progressed, may be regarded as instrumental in causing the ant to slow up and to turn toward the appropriate wall. In describing this behavior (pp. 73–79), we have shown how the kinaesthetic stimuli call out the slowing movements and the approach to the appropriate alley wall, and thus permit the contact that serves as a local adjustment by means of which the turn may be made. As learning continues, the rapidity and smoothness of this general kinaesthetic-motor adjustment, and the local contact-motor adjustment brought into play through it, greatly increase. The contact and kinaesthetic influences cannot be considered as operative in maze-orientation and learning except in a very closely integrated manner. Hence we combine them as the *contact-kinaesthetic factor*.

9. *Changes in the pattern of a previously learned maze:* Several studies were made involving local pattern changes which were introduced after original learning had taken place. We have discussed sample results

obtained from the changing of pattern *Bt1* to *Bt2*, and from the changing of *Bb1* to *Bb3*.

The experiments show that after an ant has once learned a maze, she will be able to adapt herself to a change in its pattern, in time recovering her former efficiency. This is true whether the locality involved in the altered pattern be near the nest, the center of the maze, or close to the food-box.

The essential nature of the changes in pattern introduced in these experiments was an alteration of the relationship of true path to blind alley in the locality. The introduction of new blind alleys at former 90° true path turns was also a feature. In every case, the ant tended to respond according to the former relations of the maze pathways, and became locally disoriented after this behavior proved unavailing. In the subsequent wandering, the ant often entered the unchanged portion of the maze. When this occurred, reorientation soon took place, after two or three consecutive turns had been made in the appropriate direction over the unaltered pathway.

Following a change in pattern, the ant passed rapidly through the unchanged parts of the maze, and except for the altered alleys the behavior was generally the same as before. On further trips, after passing the border of the changed region to enter the unaltered alleys, the former rapid and smooth-running movements carried the ant through the remaining alleys. Hence the initial disorientation produced by a change in pattern is confined to the changed portion of the maze.

10. *Mastery of various features of changed maze patterns:* In evaluating results, it is important that the configuration of the altered portion of the maze be carefully considered in relation to the original pattern. In the experiments, if a former turn into true pathway at a junction had been strongly favored by centrifugal swing, and thus easily established in the original learning, this response was found to persist as a regular part of the new behavior long after other errors had dropped, if it were made to lead into a blind alley in the secondary pattern. In most cases, after a considerable number of trips, there was indication that entrance into such an alley would ultimately be eliminated. Not only was there an early elimination of entrances into the second arm (although for a time the tendency to respond to this as part of a series of true path units, as in the original situation, strongly persisted), but after a considerable number of trips there was also a tendency to shorten the extent of entrance into the first arm.

In maze *Bb1*, as changed to *Bb3*, we studied the reverse of the above

condition,—namely, a blind alley turn which was originally a coerced error, and thus eliminated only with great difficulty, was made a true pathway turn in the changed pattern (p. 87f.). After this strongly enforced error had at last become eliminated in the original situation, and the direct turn into true pathway had been established, the introduction of a change in pattern which reversed the conditions (the former blind alley turn becoming true pathway), resulted in the facile restoration of the favored turn. When a return to the original maze pattern made the re-established movements lead into blind alley, the alternative behavior returned more easily than had been the case for original learning, but with greater difficulty than had characterized the elimination of entrance into the favored alley.

Other important features of these experiments included the introduction of an alternative to a former 90° turn in uninterrupted true pathway, thus making a 180° junction at which the former true pathway turned led into a blind alley. When the pattern was changed (pp. 88–94), if two arms of the original true pathway had been included in the new blind alley, the preservation of the originally established movement would now take the ant to the end of the blind alley. Soon the ant would no longer enter the second arm, and on further trips there were short and long entrances into the first arm, the former gradually becoming more frequent and alternating with trips on which there was direct entrance into the true pathway. Finally the blind alley would not be entered at all. Hence there was a tendency for the learned movements to persist, but when they led into a blind alley they were dropped in a manner similar to the elimination of a blind alley during original learning. When a return to the original pattern again made these movements lead through true pathway, the temporarily established behavior soon yielded in favor of their reinstatement. Moreover, this shift in behavior, and further adjustments necessitated by subsequent alternations of the original and the changed patterns, were made with increasing promptness.

11. *A 180° change in the direction of illumination, following original learning:* After having learned the maze with stable unipolar illumination, many ants were able to adapt to a 180° change in the position of the light source. The relearning involved in this adjustment always required less trips than were needed for original learning of the maze. The main group of the present experiments involved the introduction of such 180° changes in illumination for the trip to the nest, the change being made while the ant was in the food-box. As a control, the origi-

nal illumination was retained during the trips toward the food-box. Under such conditions, although the visual change disturbed the ant during her trips to the nest, there was no observable effect upon the behavior during runs to the food-box,—another indication of the essential independence of the responses made in passing through the maze in the two directions.

When the 180° change was made, the ant in the food-box exhibited a tendency to virtually orient herself with reference to the original position of the light. There was a tendency of this kind in passing through the maze alleys, as well, but it was not pronounced, since there was little opportunity for it in patterns *Bt1* and *Bb1*.

After a change in the direction of illumination, the greatest disorientation was found in the alleys near the food-box. Here the course was hesitant and slow, and there was considerable wandering in most cases. The disoriented ant finally passed through the later alleys of the maze by following the walls in close contact. This contact usually lessened in intensity as the middle alleys of the maze were neared, in favor of a more rapid and efficient passage through the alleys nearer the nest. The extent of the disorientation in alleys near the food-box, and the rapidity and efficiency of progress after these alleys were once passed, were found subject to individual differences.

12. *Learning and relearning of a change in illumination:* For further trips through a visually altered maze situation (direction of illumination changed following original learning), the number of returns and excess movements produced by the primary disturbance decreased, until the responses appeared again in their former smooth-running sequence. If the illumination was then returned to the original direction, there would be some disorientation, similar to that evidenced when the first visual change was made, but not as serious a disturbance, and adapted to more quickly. In this way, all four directions of illumination could be separately brought into effect, and the maze would be successively relearned under the influence of each.

13. *Multipolar illumination:* No disturbance, or a very negligible disturbance, was found to result from the combination of illumination from one quarter of the maze with that from any one or more of the other three, providing the components had been previously mastered separately. Thus it was possible to combine three previously learned directions of illumination, or four, or any two (adjacent or opposite), without introducing a serious disorientation.

14. *Alternation of unipolar with unipolar, or with multipolar illumina-*

tion: Adaptation occurred more promptly the oftener a change was made from one to another of previously learned visual situations. In addition, when a new direction of illumination was alternated with a previously learned condition, the mastery of the former situation came earlier than was the case when it was allowed to persist until learned, without any change.

III. GENERAL DISCUSSION

The recent writers on the subject of ant orientation have properly stressed the important species differences that have been proven. It is also evident that in no one species can orientation always have the same basis, and that the types of potentially effective stimuli cannot be constant.

For the individual foraging worker, the nature of the stimuli that control orientation must vary according to conditions. At times the ground is washed by rain, removing or weakening the chemical substances. Again, the terrain features may be changed, necessitating a corresponding adjustment in contact-kinaesthetic control; and the direction of illumination and other visual influences are constantly changing. Yet ants show themselves able to adapt with considerable facility to such fluctuating features of their environment.

The rôles of the various orienting factors (naming them, without respect to importance: the *visual*, *chemical*, and *contact-kinaesthetic* factors), must vary according to the environmental conditions. For example, European investigators of field orientation have found the *Formica* species relatively independent of chemical substances, yet when ants of these species must run over relatively restricted pathways, as in the maze situation, the chemical traces become important. Further, the importance of the chemical factor in field orientation varies according to the nature of the terrain.

The control exerted by the other factors is also subject to conditions. In any case, as Piéron early suggested, the kinaesthetic stimuli are of importance in the orientation of all species. Entering into a detailed study of the kinaesthetic factor, we have found its influence bound closely together with that of the contact

factor, in a control that increases in precision as the course of learning proceeds.

Vision (direction of illumination) is also an integrated part of this increasingly efficient total control, but the writer's observations and experiments show its influence to be more general than that of the other factors. Typically, a polarized illumination is effective through the visual receptors in guiding the grosser movements, especially in facilitating the principal turns that must be made in passing through the situation. Adding itself to this control, in closer relationship as learning proceeds, the influence of the contact-kinaesthetic factor comes to modify these movements on the basis of more specific effects,—i.e., determining how far the animal shall move in a certain direction, when a turn is to be made, and just how this turn shall occur, etc. In no case is it possible to separate the part played by any one of these factors, at whatever stage of the learning process, from the influence of the others. They act in close combination, but when one is removed or altered, the others are relied upon to a greater extent than before,—temporarily, if the removed or changed feature is returned or is left constant in its new condition; or permanently, if the altered element is consistently varied or removed so that it can be used no longer (e.g., removal of differential chemical control in the present experiments).

Observing in detail the course of maze-learning, the writer has been able to study the growth of the control exerted by the principal factors. The results have led to the suggestion that in experimenting upon the rôles of the receptors in field orientation, some precaution be taken to insure the opportunity of the various individuals to obtain about the same amount of experience in the situation, if their behavior is to be compared. This is necessitated by the strong indication that the proportional influence of the receptors is not the same throughout the development of orienting efficiency.

We have found ants able to learn rather involved situations, under conditions necessitating a complicated conditioning process that is constantly coming into new relationships with the influences of the receptors. Parts of the learned series of movements

may be broken down and rebuilt, or may be brought back successively into the appropriate behavior, as occasion changes the stimulating conditions. For example, in forcing adjustment to changing visual conditions, we have found a clear suggestion as to the process involved in adapting to the different positions of the sun. Similarly, in our changed pattern experiments, we have studied a type of adjustment very similar to that by which an ant changes her movements to conform to the shifting of a large tree trunk, one side of which has been used in her homegoing.

The interesting side of the learning that is involved in all field orientation of ants is not the mere fact that the animal is likely to straighten her path on successive journeys over the terrain, but is the nature of the course by which the straightening comes about—the way in which detours around objects are eliminated, and new features brought into play as guides, etc.—and the way in which the foraging ant adapts herself to the constantly changing features of a complex environment.

IV. CONCLUSIONS

1) Ants of the *Formica* species studied exhibit a relatively high degree of learning. This is shown by their ability to master a rather complicated maze in a fairly small number of repetitions, and to adapt to changes in the direction of illumination and in the maze pattern.

2) As Shepard found, there is as a rule little decrement in the maze habit due to disuse over a considerable period of time. Even after a three weeks absence from the maze, the initial error-commission is not much greater than for the last trips before the interval, and efficiency is quickly restored.

3) Although in their orientation under natural conditions, ants of *Formica* and related species do not seem to depend much upon the chemical peculiarities of the situation, when their trails are superimposed (as in the maze) the chemical traces become important. There appears to be a slight end-to-end polarization (chemical) of the maze trail, but this is not sufficiently strong to become an influence in orientation. The guiding effect of the chemical differences at crucial points (junctions of true pathway and blind alley) in the maze may be eliminated by the regular exchange of the bristol board units lining the two alternative pathways at the junctions.

4) The principle of *centrifugal swing* (p. 118, pt. 6) is of great importance in determining maze behavior, even during the first trips made by an ant. By taking the function of this factor into account in designing mazes, it is possible to 'coerce' entrance into certain blind alleys, and prevent entrance into others.

5) When entrance into a blind alley is favored by the pattern relations of the maze (introducing the influence of centrifugal swing), many maze trips are required for the elimination of this behavior. The dropping of these enforced errors follows a typical course (p. 119, pt. 7), which mainly depends upon a transition in the contact-kinaesthetic control of movements.

6) After the original maze pattern has been learned, a local change in pathway relations produces disorientation, but not in the unchanged portions of the maze. In a relatively short time efficient maze passage is re-established, a portion of the formerly effective series of movements having been modified by the conditioning effect of the altered alleys.

7) When, in the original pattern, entrance into the true pathway alternative at a junction has been favored by centrifugal swing (see 4 and 5 above), and in the changed pattern the same movements lead into a blind alley, they persist strongly in the new situation. In time, however, the second arm of the new blind alley is not entered. After a great number of trips, the first arm tends to be entered a shorter distance, forecasting its ultimate elimination.

8) When entrance into a blind alley is favored during original learning, and the movements leading directly into the true pathway alternative are therefore established with great difficulty, the latter behavior is relatively easily eliminated when a change in pattern makes it lead into a blind alley. This result is to be definitely contrasted with point 7, above.

9) When a pattern change makes a former 90° turn lead into a blind alley (by introducing a true pathway alternative), the blind alley tends to be regularly entered after the change is made, but after a time is eliminated in favor of a direct turn to the newly introduced true pathway. In any case, such a secondary blind alley is eliminated with far less difficulty than is the type referred to in point 7.

10) Ants of these *Formica* species are able to relearn the trip to the nest through the maze under conditions involving the successive illumination of the maze (until learned) from each of the four principal directions. After having been learned singly, no combination of two or more of these unipolar visual situations proves very disturbing to the ant whose behavior is being studied.

11) The plasticity with which ants are able to adjust themselves to changing conditions is definitely shown by experiments which involve the alternate introduction of original and partially altered maze patterns, and by experiments in which shifts are made among visually different maze-situations. In either case, the oftener the different conditions are alternately introduced, the greater the facility with which the animal adapts to the changes.

12) Passage through the maze in the two directions (from nest to food-box, and from food-box to the nest) involves essentially disparate series of movements, each a closed system, under control of the factorial (sensory) relationships peculiar to the trip in that direction.

13) During original learning, the direction of the principal illumination is of great importance as a general control of movements. The contact and kinaesthetic influences become closely integrated, and assume a gradually increasing control of local adjusting movements. They are especially effective in producing a rapid and smooth-running series of responses for passage through the alleys furthest from the starting point (i.e., for alleys nearer the nest, on the trip to nest).

14) The orienting factors are operative according to the extent permitted by the environmental stimuli, and their respective influences vary according to the stage attained in the learning. The studies previously made on the field orientation of ants have suffered through not taking these facts adequately into account. The homegoing ability of ants has been viewed as altogether too static a process, mainly because of a general neglect of the influence of learning.

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APPENDIX I

The record of ant 'z', F. subsericea, from Jan. 17 to May 5, 1927. (See Fig. 7 and pp. 53-55. Also see note 38)

Trips to food-box

Jan. 17 . . .

The first trips involved the usual primary errors (retracing in open true pathway, from 90° and 180° turns, and from blind alleys), but these were dropped relatively quickly. On trips 8-12 a sudden series of impacts in the next room produced an emotional excitement centering in situation 4-5. This disturbance spread to other parts of the maze, persisting somewhat on later trips. On trip 50 the ant was greatly disturbed by a recurrence of the intense vibration (clanging of radiator), which started suddenly and lasted but a short time. The major effect of the excitement again was seen in the vicinity of situation 4-5, although there were some errors in other parts of the maze. On trip 56 this trouble again appeared, causing hesitant and jerky progress through the maze. The ant was excluded from the maze for ten minutes. After this interval, she passed through the maze in a relatively rapid and unexcited manner.

Jan. 18 . . .

The progress during the trips to food-box was uniformly slow and irregular. However, on the last trip the ant quickened her pace and made fewer errors.

Trips to nest

On the first two trips no food was carried, although each time a piece was picked up at first. On trip 25 'z' returned from alley 7b to the alleys of situation 9, somewhat disoriented. . . . On trips 67-68 the experiment involved a 90° change in the direction of illumination. There was a marked disturbance during the time the change persisted, but the ant passed to the nest with little difficulty when the original condition of illumination was restored. This experiment had no observable effect on the trips to the food-box.

Note the rapid decrease in errors, although the trips to food-box, with the exception of the last one, were not good. No food was carried on the first trip to the nest. Trips 3 and 4 were quite rapid and correct, after alley 9f was passed.

Trips to food-box

Jan. 19 . . .

On trip 3 'z' suddenly met another ant in alley 8. She stopped suddenly, disturbed, and began to palpate the corner of the alley with her antennae. . . . On trip 6 the opening of the entrance as the ant was coming across the bridge appeared to disturb her, since her progress to the food-box was jerky and excited. The disturbance was particularly noticeable in situation 4-5, where there was a conditioned disturbance on further trips.

Jan. 20 . . .

On trip 2 the ant failed to pass further than alley 9e, turning there to run rapidly and without error to alley 1. She quickly turned at the end of alley 1 and went back toward the food-box, entering alleys 4 and 6a, and having difficulty at junction 8-9, again failing to pass alley 9c. 'z' finally proceeded from the maze, going correctly except for retracing from alley 3a to 3c 1/2. On trip 3 her passage was correct as far as junction 8-9 (excepting entrances into blind alleys 4 and 6, as usual), but here, after considerable difficulty, she turned to pass back toward the nest. At alley 5b she again turned toward the food-box, and finally reached it after a number of errors were made. On later trips, the number of errors was reduced, and the mistakes due to the exchanges in linings at the junctions rapidly decreased. During the 13th and last trip the ant showed evident signs of fatigue, failing to reach the food-box.

Jan. 21 . . .

The ant came into the maze fairly rapidly, as usual, and entered alleys 4 and 6, but at junction 8-9 and its vicinity she appeared disoriented. She wandered to alley 9c, and then turned

Trips to nest

No food was carried on trip 1, and all of the difficulty was experienced in the alleys of situation 9. After the first trip, excepting occasional errors at the 180° turns in situation 9, the trips to the nest were rapidly and smoothly made.

Food was carried on the first trip, a fairly bulky load composed of a number of adhering pieces. The ant could not use her antennae effectively, and hence over-ran alley 5b into alley 6. After trip 2, the runs to the nest were uniformly correct and rapid, except that on trip 12 there were four successive returns to the food-box from alley 9e. Although 'z' carried no food on this trip, after leaving alley 9c her progress was rapid and without error.

Trips to food-box

to proceed rapidly from the maze, the only error being a minor retraceal in alley 5.

Jan. 22 . . .

On all three trips 'z' encountered difficulty in making the 180° turns in situation 9. The exchange of the alley 4 and alley 5 linings caused the ant to pass directly into alley 5. On trip 4, the last trip of the day, she passed correctly to junction 8-9 (except for entering alleys 4 and 6, as usual), but failed to reach the food-box.

Jan. 24 . . .

On trip 1 the ant did not enter alley 6 or 8, but passed quite rapidly to the food-box. On trip 2 she entered all three blind alleys, but did not pass alley 9c. During trip 3, 'z' was very erratic in her behavior near junction 4-5, and retraced each of these alleys before passing on toward the food-box.

Feb. 3 . . .

With subsequent trips the ant made increasingly rapid and efficient runs. From the start of this day's trips there was little difficulty in making the trips to the nest. For the trips to the food-box, errors due to hesitation at turns, to disturbance produced by exchanges of linings at the junctions, and to difficulty in the alleys of situation 9, quickly disappeared. There was an increasing tendency to eliminate primary entrances (direct entrance from the preceding unit of true pathway) into blind alleys 4, 6, and 8. This is indicated by the regular descent in the 'trip to food-box' error curve. After trip 40 the

Trips to nest

A large load of food (several adhering pieces) carried on trip 1 resulted in over-running into alley 6, hesitation at junctions and at turns in true pathway, etc. On trip 2 the ant did not carry food, and displayed rather erratic progress, including three retranceals from 90° turns. On trip 4 'z' did not carry food, but returned from alley 9c to the food-box four times before leaving the made.

On trip 1 ant 'z' did not carry food, and was erratic in her behavior, returning to the food-box five times from alleys of situation 9. She did not reach the food-box on trip 2, but turned back at alley 9c, to make only one error (over-running into alley 6) in passing to the nest. On trip 3 the ant was erratic until junction 6-7 was passed, and then continued rapidly and correctly to the food-box.

Trips to food-box

number of errors increased, the direct effect of a rather intense vibratory disturbance (chairs pulled over the floor in the next room) which led to jerky, erratic behavior on the part of the ant. The disturbance produced irregular mistakes at the junctions, and there was difficulty in passing 90° turns such as 9c and 9e.

Feb. 7 . . .

The curve for Feb. 7 starts somewhat above that for Feb. 3, but soon falls below the level of the latter. The substitution of a new alley lining in 7b first caused some disturbance when this alley was reached, but the trouble disappeared with further exchanges of the old and new linings. Primary entrance into alley 8 was completely eliminated and the tendency to enter alleys 4 and 6 showed distinct signs of disappearing. There was only one trip after the change to pattern Bb3 was made.

Feb. 10 . . .

Six entrances were made into the Bb3 pattern, but the food-box was reached on only the third and fourth of them. The ant's behavior was much the same as before until the changed part of the maze was reached, but when the altered alleys were entered there was evident disorientation.

Feb. 16 . . .

'2' did not reach the food-box on the first three trips. Then the Bb1 pattern was restored, and there was great difficulty in passing through the alleys of situation 9. There was again an initial difficulty due to the tendency to enter alley 8. The more irregular errors dropped rapidly, and the above-mentioned ones soon showed signs of elimi-

Trips to nest

Although separated by an interval of four days, the first trips for Feb. 7 were about as efficient as the last ones for Feb. 3. Note the regularity that characterizes the curve for the trips to the nest. For the most part these runs were correct, although there was an occasional error due to over-running into a blind alley.

During the first three trips, although the food-box was not reached, the ant always returned rapidly to the nest after turning back from the changed portion. After pattern Bb1 was reinstated, the irregular errors that were first made in the changed alleys were seen to drop out rapidly. The slight tendency to retrace in alley 9f (C)

Trips to food-box

nation. The first changes in pathway linings caused trouble, but this soon disappeared, although the experiment of waiting until the eighth trip to begin the changes protracted the disturbance. On trip 18 there were additional errors, due to a disturbance produced by exchanging the linings of alleys 8 and 9. This exchange caused alley 8a to be entered, although previous to this there was a tendency toward the shortening of entrances into alley 8. . . . Beginning at trip 34, the rise in the error curve is due to a continued series of intense vibrations that came from the next room. This disturbance led to very erratic behavior, particularly in the vicinity of situation 4, where there were twelve successive retracements on trip 34. After four trips, the vibratory disturbance stopped, but the excited and erratic behavior continued. This was particularly effective in producing several errors in situation 4-5 on most of the remaining trips of the day. . . . On trip 66, while climbing on the wall in the corner of alleys 4-4a, the ant happened to catch her right antenna between the glass and felt wall cover. Although the member was extricated at once, the behavior of 'z' on further trips became much more excited when this part of the maze was reached. The maze trips were allowed to continue, in order not only to permit observation of the course and effects of this emotional behavior, but study of its possible influence on the *trips to nest*, as well.

In this connection it should be added that ant 'z' was much more subject to this type of disturbance than were most *F. subsericea* ants. More than once, when this ant was passing through the maze while other individuals were present, a vibratory disturbance would cause her to behave in an excited and

Trips to nest

persisted for some time, but finally disappeared. It is interesting to note that although the disturbing vibrations (beginning on trip 34) lasted through the *trips to nest*, as well, there was little effect here, and the erratic error-committing behavior was confined to unladen trips to the food-box. On the last few trips, after a further emotional effect had been added through the accident in the corner of alley 4-4a (see *trips to food-box*), there was still no great effect upon the trips to nest. As soon as the ant had gotten food, on any trip, she was a 'changed animal,' although when again she made the trip to food-box, the erratic behavior was again observed. . . . On the last trip there were three successive returns to the food-box, before 'z' left for the nest without a burden.

Trips to food-box

erratic manner, while affecting the other ants but little.

Feb. 17 . . .

The effect of the former disturbance in situation 4 was again observed, producing such errors as primary entrances to 4, usually to the end of alley 4a, returns from alley 5 to 4 and from 4 to 5, etc. Except for their difficulty, the trips to the food-box were very regular, showing a distinct tendency toward the elimination of primary entrances into alleys 6 and 8. The latter behavior had dropped completely by the 18th trip for the day. After trip 14, alley 4 was entered regularly to its end, without any returns, but with a direct passage through situation 5. On further trips, there was some evidence of the former emotional behavior in situation 4, but although the ant committed the characteristic errors there (running about a few times near the 4-4a corner on each trip), her behavior lacked the earlier intense excitement.

Feb. 18 . . .

There were no errors, excepting those in situation A-B (8-9 in Bb1). On the first trip 'z' had considerable difficulty in this situation, and made a number of returns, but on the second trip there was only one entrance into alley B prior to her direct passage through situation A.

Trips to nest

Note the fact that from the start, the exits from food-box to nest were rapid and correct. This behavior may be contrasted with that for the corresponding trips to the food-box.

Following the 34th trip, the change to the Bb3 pattern produced great difficulty, based upon the persistent tendency to enter situation C (9f, etc., in Bb1) and to wander in the vicinity. The trouble was seen to gradually decrease.

On each trip there was a primary entrance into alley C, followed by a correct run to the nest. A very interesting feature of the second trip was the following: Leaving the food-box without food, the ant entered alley C, then turned into situation A and passed correctly through the maze to situation 2-3. In turning the corner from alley 3a into 3, she failed to 'hug' the nest-ward wall of alley 3 as closely as usual, and hence over-ran the entrance to alley 1, and passed into alley 2. Upon reaching the end of alley 2, the ant turned rapidly, hurried back through the rest of the maze, and ran correctly to alley A2, except for entering one-fourth way into alley 4.

Trips to food-box

Feb. 22 . . .

To permit study of the effect that the responses established for alleys *B* and *C* ('food-box' and 'nest' trips, respectively) might have upon behavior in maze Bb1, this pattern was again introduced. On the first trip after the change there was considerable difficulty at junction 8-9, and two returns from the 180° turns were made (9c and 9e), but on the second and third trips the only difficulty was a short return from 9e. The first exchange of the 8-9 linings on the third trip not only caused alleys 8 and 9 each to be retraced twice, but also produced as a secondary effect a considerable amount of difficulty at the 180° turns in situation 9. This difficulty soon disappeared. The next two exchanges of the linings at this junction brought back the disturbance, to a slighter extent, and after that there was no trouble. During the last four trips there were no errors in this situation, and alley 9 was entered directly each time. Again, the promptness of this adaptation may be contrasted with that to the previous change from pattern Bb3 to Bb1 (Feb. 16). The five day interval since the last considerable number of maze trips seemed to have brought back a tendency to enter the three blind alleys, although in all three cases, and especially in that of alley 8, there were prompt and distinct signs of shortening and elimination. On the last two trips, a vibratory disturbance caused evident excitement, and the maze was closed.

Feb. 23 . . .

There was a noticeable tendency to behave erratically, particularly in the

Trips to nest

At alley A2 she hesitated, partially entered A3, and then turned quickly to pass correctly to the nest.

As the curve shows, the initial disturbance in alley 9f (C) which followed the change to pattern Bb1 was very quickly eliminated. In fact, after a slight retracement was made on trip 6, the only other error occurred during trip 9. This condition is to be strongly contrasted with the slower elimination of such errors on the earlier return from pattern Bb3 to Bb1 (Feb. 16).

On the first few trips there was some tendency to make irregular returns

Trips to food-box

alleys near the nest. This appeared to exist independently of exchanges in alley linings, except at first, when the exchanges tended to exaggerate the excitement at the junctions. Later, however, when there was no longer any observable effect produced by the exchanges, the irregular crawling on walls, and other erratic activity, tended to persist. The entire passage to the food-box, especially through alleys near the nest, was characterized by a jerky, hesitant motion. As far as could be determined, this behavior had no extraneous basis. Since the ant continued to run in this manner in passing to the food-box, the maze was closed after trip 14.

Feb. 25 . . .

The ant tended to hesitate near the beginning of the maze, but ran correctly and rapidly after situation 4-5 was passed. Her motion was at first quite similar to the jerky progress observed on the preceding trips, and involved zig-zagging from side to side in passing through the alleys.

March 1 . . .

On trip 6 'z' carried a fairly large piece of earth through the maze, and deposited it in the food-box, returning with a small particle of meat, as usual. . . . The initial rise in the curve is due to the usual temporary disturbance produced by the first exchanges in linings at the junctions. Later, the ant's progress to the food-box became more regular, and the tendency to enter the blind alleys for even a short distance began to disappear. After trip 18, a change to pattern *Bb3* produced some disturbance at junction *A-B*, due to a persistent tendency to enter alley *B* (9), but 'z' regularly passed on through

Trips to nest

from 90° turns, etc., but this behavior disappeared after a time.

Only one trip was made. After leaving the food-box, the ant ran to the corner of alley 9c with a piece of meat, dropped it there, and returned to the food-box. Then she passed to the nest without food, correctly save for a slight hesitancy at the corner of alley 7.

Note the very small number of errors, from the start, and the fact that the few irregular ones quickly disappeared. Contrast this with the record for the *trips to food-box*.

Trips to food-box

situation *A* after one or two short entrances.

March 7 . . .

The characteristic errors appeared at junction *A-B*. First there would be an entrance into *B*, then wandering, and finally a passage through situation *A* to the food-box.

March 8 . . .

Note the low point at which the error curve begins, in spite of the fact that there had been only three trips (on March 7) during the preceding week, and a total of only nine trips since the Bb3 pattern was last introduced. . . . On trip 6 there was more difficulty than any previous passage had given, at junction *A-B*. On the next trip the linings were exchanged at this junction, and alley *A* was directly entered from 7b, followed by a correct passage through the remaining alleys of the maze. On the following trips, there was still a tendency to enter alley *B*. The rise in the error curve at trip 14, and again at some of the later trips, together with the failure to improve much, may be attributed directly to the vibrations produced by the clanging of a radiator in the next room. . . . On only two of the trips following 16 was there difficulty in situation *A-B*; the other runs being rapidly made.

April 2 . . .

After a few scattered trips on intervening days, there was a steady decrease in errors on April 2, although there had been an interval of almost four weeks since any number of maze trips had been made on any one day (four trips on 3/4, and for the rest only two or one trip each day). Notwithstanding this, in ten trips on 4/2 the

Trips to nest

'2' rapidly eliminated errors incident to situation *A4-C*, retaining the tendency to enter *C* itself.

There was steady progress in eliminating the errors incident to situation *A4-C*, marked by a decrease in the number of primary entrances into alley *C*, in the distance of the primary entrance, and in the number of retraceals made after the alley was first entered. On trip 19 '2' spent some time in the food-box, due to the fact that she first picked up a rather dry piece of food, which continually escaped from her mandibles. On this trip, as on the last one for the day (27), there was a number of returns to the food-box from alleys of situations *C* and *A*. Excepting these errors, improvement occurred regularly to the end.

There was a regular decrease in the errors made. The tendency to retrace in situation *A4-3-C* was soon eliminated.

Trips to food-box

errors had been reduced almost to the level attained on March 8. Despite the fact that the quarter of the maze near the food-box had involved the earlier pattern changes, it did not give a disproportionate amount of difficulty in the relearning.

April 13 . . .

After an eleven day interval, there was very little decrease in the efficiency of the ant's maze-running, and during the first ten trips her errors were still further reduced. The direct entrance into *A* instead of into *B* (from 7b) soon was the rule, and there was a gradually increasing tendency toward the elimination of primary entrances into blind alleys 4 and 6.

May 5 . . .

In spite of the fact that 'z' had not been in the maze for twenty-two days, her initial errors were surprisingly small in number, and their elimination was a very rapid one. On her first trip there were no retraceals whatever, and there was no difficulty in passing through the alleys near the food-box (only 29 seconds required for this trip). . . . The usual minimal errors (entrance to alleys 4 and 6, and the tendency to enter alley *B*) appeared. Alley 4a was usually entered its full length, but alley 6 was entered a very short distance. On the second trip alley 6 was not entered at all, and alley 4 only one-sixth of its length. . . . The changed portion of the maze (alley situation A, etc.) was passed through without error on the first three trips. The exchanges in alley linings at the junctions then began to cause some difficulty in the alleys near the nest, but this soon disappeared. The only error on any of the last five trips was a short entrance into alley 4.

Trips to nest

The number of errors decreased rapidly. The tendency to retrace in the vicinity of situation A4-C, which accounted for most of the early errors, rapidly disappeared. On trip 33 'z' retraced rapidly in alley A3, once to alley A4. This accounts for the rise in the error curve at that point.

On the first trips the errors were confined to the alleys nearer the food-box. The tendency to enter alley *C* again appeared, as did the tendency to retrace in A3 and to hesitate on entering alley 7. After leaving alley 7b, however, the passage was consistently rapid and smooth, from the first trips. Later, the elimination of the tendency to enter alley *C* began to cause retraceals in nearby portions of the maze, but even these errors dropped relatively rapidly. For the last four trips, the only error 'z' made was a short return in alley 7a on one trip, caused by bumping into the corner of this alley in her great speed. In view of the twenty-two day absence from the maze prior to these trips, the small number of initial errors and their rapid elimination make the accomplishment a remarkable one.

APPENDIX II

In connection with the effect of food-carrying on behavior in the maze (p. 65) there is another important question. Bethe made the statement (repeated by Loeb in his "Comparative Physiology of the Brain and Comparative Psychology," p. 121) that a laden ant automatically takes the trail to the nest, an unladen ant the trail from the nest. The situation is actually much more complex than this simple statement implies. One would take Bethe to mean '*laden* with food, or a larva,' but surely the mere fact of being laden is not crucial. Ants carry their larvae in moving from one nest place to another, and during normal nest activity carry earth and refuse from the nest to a refuse place or "kitchen midden" (Wheeler). The writer repeatedly has seen ants carry particles of earth and other nest refuse into the maze, or even to the food-box, after learning the maze. Hence it is the nature of the load carried that determines behavior.

A further question has been asked: "Can an ant carry food only toward the nest, provided she has learned the way to and from the nest?" This question can be answered from maze observations. If, after once learning the maze, an ant on her way toward the food-box finds food in an intermediate alley, it is not certain that she will turn at once and proceed to the nest. In some cases, after a short period of wandering in the vicinity, the ant passes to the nest with the food, but this does not occur every time. It can be said that the course taken usually depends upon how well the maze has been learned, upon the location of the alley in which food is picked up, upon the amount of hesitation involved in acquiring the food, and upon the position assumed by the ant at the time.

The writer has often seen ants leave the food-box without carrying a burden, and pass rapidly and correctly to the nest. (This may occur after the food has become too dry, after a great many trips have been made, on the first one or two trips of a new day, or after a longer interval in the nest between trips.) Oftentimes, a food-carrying individual has been seen to fail in making a turn when nearing the nest, and after a short period of disorientation to pass rapidly toward the food-box, still carrying the burden. Hence a laden ant may pass correctly through the maze to the food-box, and an unladen ant may pass correctly to the nest. The writer has found that the carrying of food has much importance in determining the assumption of progress toward the nest, but to say that the passage cannot be undertaken without food simplifies the situation in a quite unwarranted and misrepresentative manner. The coordinated responses incident to passage in either direction may be made whether or not food is carried.

